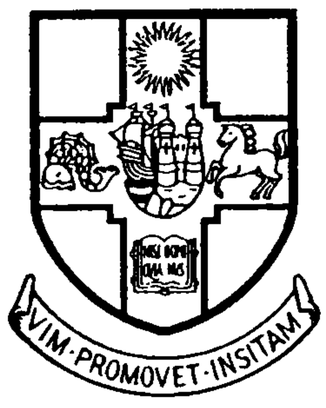
Author:
Lane, Abigail Ann

Title:
Patterns and dynamics of palaeozoic marine biodiversification

PATTERNS AND DYNAMICS OF PALAEOZOIC MARINE BIODIVERSIFICATION



ABIGAIL A. LANE

A dissertation submitted to the University of Bristol in accordance with the requirements of the degree of Doctor of Philosophy in the Department of Earth Sciences, Faculty of Science.

January 2003

Word count (text only): 48,489

ABSTRACT

Key aims of recent palaeobiological research have been the construction of Phanerozoic global biodiversity patterns, and the formulation of models generalising such patterns and proposing mechanisms of biodiversification. Accurate biodiversity estimation methods are crucial to these endeavours. The taxic and phylogenetic methods of estimating diversity are tested using simulated phylogenetic trees. The phylogenetic estimate is found to be superior at capturing real patterns of diversity in analyses of large clades with many extant representatives. However, skew introduced into patterns prior to mass extinction events indicates that the method is inappropriate for studies of extinct groups, particularly those containing few taxa or suffering many significant extinctions.

The exponential and logistic models for the diversification of metazoan life are reviewed. The Palaeozoic plateau – the apparent equilibrium in marine familial diversity from the Mid-Ordovician to the Mid-Permian – is the strongest evidence for the logistic model of diversification. Three interpretations of the plateau are suggested and evidence for each sought using large compendia of taxonomic range data, and computer simulations. A Palaeozoic equilibrium is a feature of marine diversity curves at ordinal, familial and generic level, although it becomes less apparent as the taxonomic hierarchy is descended. A species-level model predicts an overall exponential growth form. It is unlikely that a large diversity radiation followed by an apparent equilibrium period could be produced by purely stochastic behaviour of origination and extinction rates. Tests for diversity-dependence within empirical data indicate that the Ordovician radiations were driven by a deterministic origination rate, but that the plateau itself is characterised by random rates of origination and extinction, with no evidence for an ecologically determined upper-limit to diversity.

Long-term competitive displacement of higher taxa is a faunal turnover mechanism associated with the logistic diversification hypothesis. Models of a proposed macroevolutionary displacement suggest a reduction in articulate brachiopod numbers may have been produced by competition. No evidence is found supporting the hypothesis that this reduction was a product of interactions with bivalves.

ACKNOWLEDGEMENTS

I thank my supervisors, Profs. Michael J. Benton and Derek E. G. Briggs for their support during my time at Bristol, in particular Professor Benton for his guidance and encouragement, and Professor Briggs for his thorough editing of thesis drafts.

For research collaboration I would like to express my gratitude to Dr. Paul N. Pearson for the opportunity to rewrite and use a computer simulation of his creation, and Dr. Christine M. Janis of Brown University for useful discussions on the concept of ghost ranges, and for access to notes and results produced by the late Professor J. John Sepkoski. I would also like to acknowledge Dr. Janis for granting permission to use, and Dr. Michael Foote at the University of Chicago for providing me with Sepkoski's unpublished compendium of marine fossil genera. As well as to Mike Foote, my thanks go to Professor Leigh Van Valen, Dr. Peter Wagner and Shannan Peters for extremely useful discussions and advice during my visit to Chicago, and also to Al McGowan for making me feel welcome while I was there.

This research was supported by a Natural Environment Research Council studentship and fieldwork grant (04/99/ES/16). I also received finance from the Bob Savage Memorial Fund allowing me to present aspects of this research to the 2001 Palaeontological Association meeting in Copenhagen.

For their friendship and help I must mention all at the Department of Earth Sciences, in particular Luisa Brana, Susan Couch, Claire Horwell, Sarah Tibbs, and Debbie Wharton. And finally to Jim Lane for his unfailing support, words of wisdom, and proof-reading above and beyond the call of duty, my thanks.

AUTHOR'S DECLARATION

The work in this dissertation is original except where indicated by special reference in the text. Any views expressed in the dissertation are those of the author and in no way represent those of the University of Bristol.

Abigail A. Lane, January 2003.

CONTENTS

LIST OF FIGURES

Chapter 3. The Palaeozoic plateau – an artefact of taxonomic level?

Chapter 4. The Palaeozoic plateau – a stochastic structure?

LIST OF TABLES

CHAPTER 1. INTRODUCTION TO PHANEROZOIC BIODIVERSITY MEASUREMENTS AND MODELS

A major theme of recent palaeontological research has been the construction of global palaeobiodiversity patterns and the search for general laws and models describing such patterns (Miller 2000). From this work have emerged several conflicting theories of Phanerozoic biodiversification, in particular whether life has followed a growth pattern that is expansionist (e.g. Valentine 1969; Walker and Valentine 1984; Signor 1985; Benton 1991, 1996) or equilibrial (e.g. Raup 1972; Sepkoski 1978, 1979, 1984; Carr and Kitchell 1980; Alroy 1998). Debate also surrounds the macroevolutionary mechanisms underlying these hypotheses, such as the concept of "evolutionary faunas" (Flessa and Imbrie 1973; Sepkoski 1981; Sepkoski and Miller 1985), diversity-dependent origination and extinction rates (Flessa and Levinton 1975; Sepkoski 1978, 1979, 1984; Alroy 1998; Foote 2000a, b), and high taxonomic-rank competitive displacement (Miller and Sepkoski 1988; Sepkoski 1996a). An understanding of past biodiversification patterns is essential to provide the context required for the assessment of current biodiversity and the effect of human activity upon the biosphere.

1.1. The concept of biodiversity

The quantification of biodiversity, or the variety of life, is an attempt to discover the range of genetic, ecological and morphological complexity within an ecosystem. At its simplest, diversity is usually defined as the number of *species* of organism extant within a specified time and space. Species are taken as the base unit of biodiversity because, through the biological species concept, they are assumed to have a biological reality beyond simply being a grouping of individual organisms convenient for the purposes of counting. Hence, an assessment of species diversity informs us of the number of ecological and evolutionary opportunities there have been for life to exist or to have existed in a particular time and place. Such opportunities are not equally spread throughout the animal kingdom, as evidenced by the highly speciose nature of some higher taxa when compared to others.

When assessing ancient biodiversity, we make the assumption that palaeospecies are equivalent to their extant counterparts, despite the impossibility of applying tests of the biological species concept to fossils. Because both palaeospecies and neospecies are

generally defined by morphological characteristics, the diversity of species may also give some measure of *disparity*, the variety of morphology among organisms. This is not an exact measure, however. Some higher taxa consist of highly similar species, while others contain species that are morphologically distinct. This is in part a consequence of varying taxonomic practice across different groups. The scales of biodiversity assessment are commonly divided up into local (*alpha*), neighbourhood (*beta*) and regional (*gamma*) (Whittaker 1972), to which can be added the *global* scale, although there are no absolute delineations between these categories.

The recognition and naming of species is the basic concept of taxonomy, and the grouping of species into higher ranks of taxa achieves a classification. The ranks of the classification of life currently conform to the Linnaean system, hierarchical levels of genus, family, order etc. This system has the advantage of being universally known and used. It has the disadvantage of forcing species groups into a structure not necessarily reflective of evolutionary process. The variety of life, having arisen by a process of descent by modification, is comprised of a sequence of nested ancestor-descendent trees. Such trees do not fit easily into a ranked scheme of classification. This has prompted attempts to implement 'rank-free' systems such as the PhyloCode concept (Cantino et al. 1999). The Linnaean binomial and hierarchical rank system, however, remains the classification scheme recognised by the international codes of nomenclature (Sneath 1992; Greuter et al. 1994; International Trust for Zoological Nomenclature 1999), and has the advantages of simplicity and familiarity (see Benton 2000 for a defence of Linnaean classification). The diversity of higher-ranked taxa is a common method of assessing the variety of life in the absence of adequate species data. Such analyses are based on the assumption that entities such as genera and families have some kind of biological meaning in their own right (e.g. Bottjer and Jablonski 1988), or that the patterns uncovered at higher taxonomic ranks reflect the pattern at species level (e.g. Sepkoski 1978, 1979). The actual methods of constructing a taxonomic classification are varied, from the traditional and authoritarian, to the more objective methods of phenetics and cladistics. While these various methods are not of direct use in the discovery of diversity patterns, the considerable arguments surrounding them are of great indirect significance when assessing the quality and usefulness of the data under analysis (see Section 1.2.3. below).

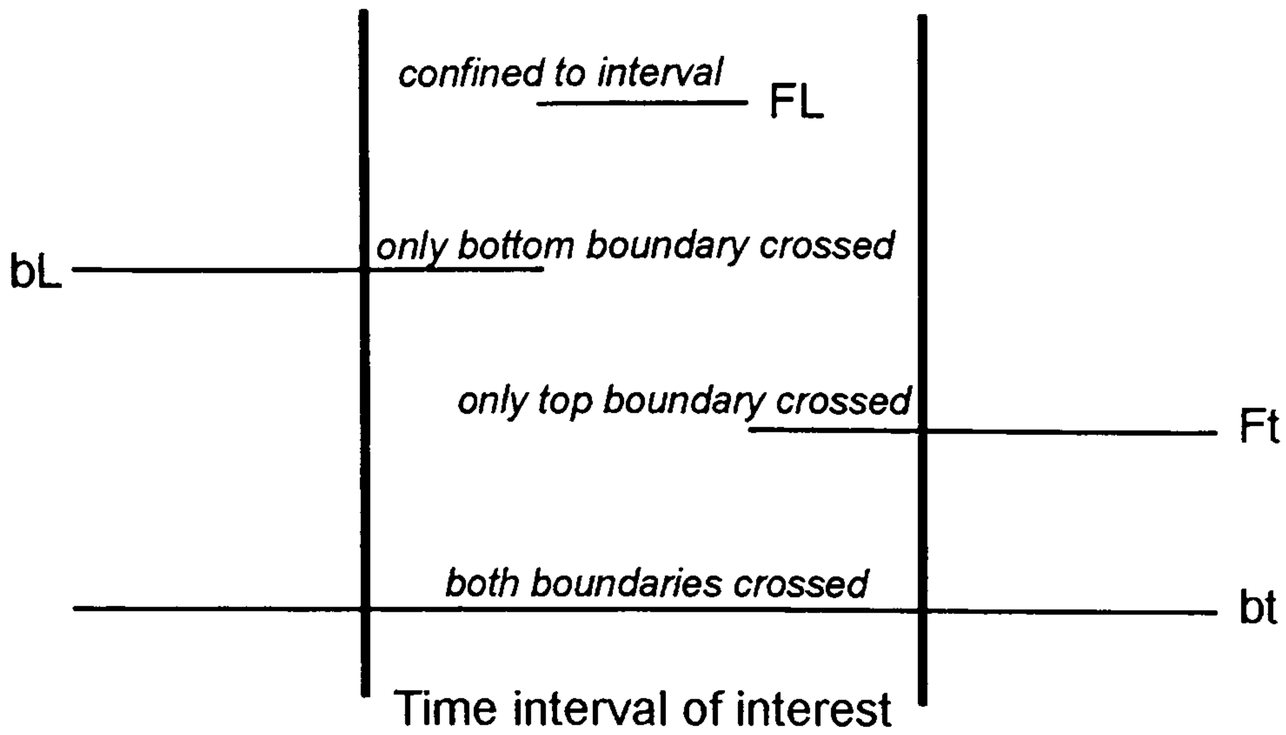
1.2. Measurements of biodiversity

The most common method for assessing ancient biodiversity is the *taxic* or 'taxon-counting' approach (Levinton 1988). At its simplest this involves splitting a time period under investigation into discrete intervals or bins, and counting the number of taxa that have a fossil record presence within each interval. This is achieved either by direct assessment, i.e. counting the number of fossil taxa found in each unit of a stratigraphic section in the field, or by taking information about fossil taxon occurrences from the scientific literature. The latter method is common for large-scale investigations over prolonged time periods, or large geographic areas where a fieldwork program to obtain the information is not feasible. For such analyses, which search beyond local taxonomic immigration and emigration to find the patterns of global originations and extinctions, the 'range-through' method is common. In this a taxon is assumed to be extant for the entire time period between its first and last appearance in the fossil record. Hence it is counted in every interval between these points, even if it does not actually have a fossil presence in them all. This eliminates so called *Lazarus taxa* (Fara 2001), those which seem to go extinct only to re-appear several intervals later, although an assessment of the amount of gap in the range of a taxon can be a useful tool in analyses of the completeness of the fossil record (Solow and Smith 1997).

In the research presented here, the *standing diversity* or simply *diversity* of a time interval is the total number of taxa that are present in that interval, either as an actual fossil occurrence or an implied presence using range-through data. In addition to the standing diversity, the number of originations and extinctions within each interval is defined as the number of taxa that appear first or last in the fossil record respectively during that interval. From these basic data a number of further statistics can be calculated. These include rates of origination and extinction which are normalised for interval length (*total* rates) and standing diversity (*per-taxon* rates), both of which have an effect on the numbers of originations and extinctions found in a chronostratigraphic interval.

An alternative method for summing standing diversity, using what has been termed *boundary crossers* (Foote 2000a, b) has been used in recent studies (Alroy 1998, 1999; Bambach 1999; Foote 2000a, b). Figure 1.1 explains this concept.

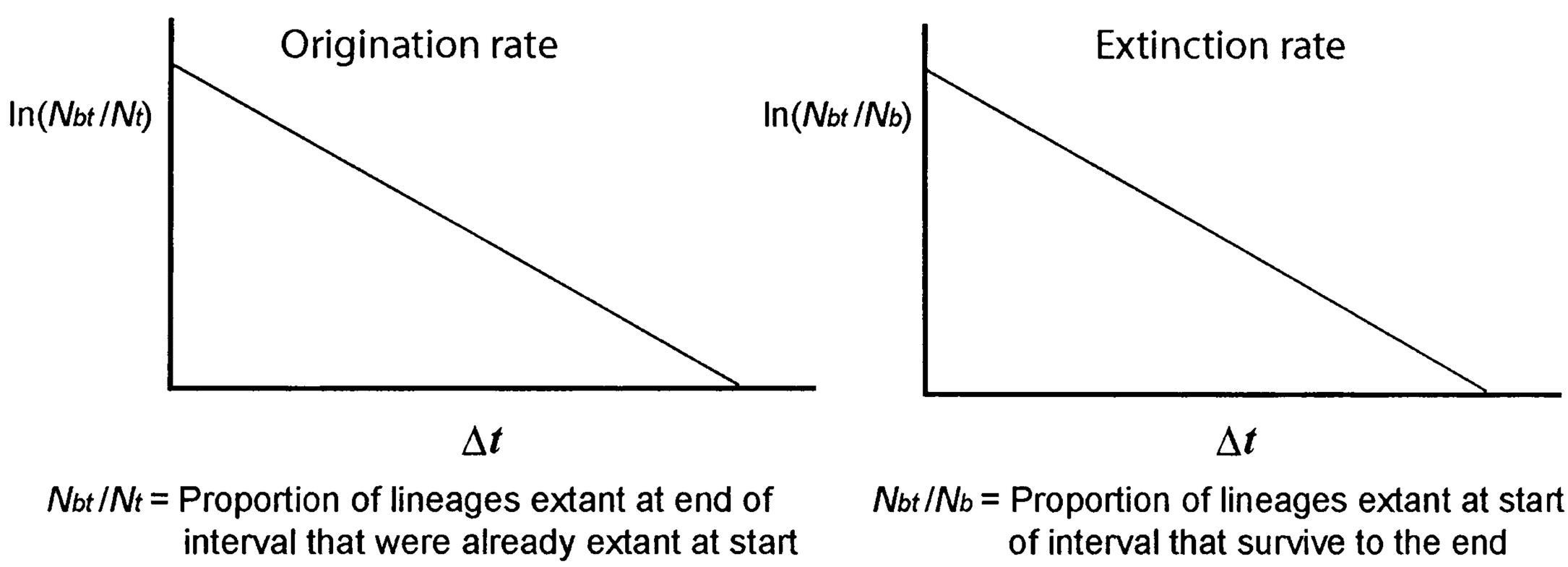
A



N_{FL} = number of taxa confined to interval
N_{bL} = number of taxa crossing bottom boundary only
N_{Ft} = number of taxa crossing top boundary only
N_{bt} = number of taxa crossing both boundaries

N_b = total number of taxa crossing bottom boundary ($N_{bt} + N_{bL}$)
N_t = total number of taxa crossing top boundary ($N_{bt} + N_{Ft}$)
N_{tot} = total diversity of interval, excluding singletons ($N_{bt} + N_{bL} + N_{Ft}$)

B



N_{bt}/N_t = Proportion of lineages extant at end of interval that were already extant at start

N_{bt}/N_b = Proportion of lineages extant at start of interval that survive to the end

FIGURE 1.1. Diversity and rates calculated using the 'boundary crosser' method. (A) The four fundamental classes of taxa with a presence during a stratigraphic interval. Measures of diversity and rates are derived from these classes plus the combinations shown (from Foote 2000a). (B) The ratios shown (the proportions of standing diversity *not* originating or going extinct in the interval) decay exponentially with increasing interval time length. Hence, the logarithms of the ratios decrease linearly with time and the magnitudes of the slope gradients are equal to the origination and extinction rates.

In summary, the boundary crosser method uses only those taxa which originate before and extend beyond the end of each stratigraphic interval for which diversity is being assessed. This method automatically excludes taxa that have ranges confined to a single interval (singletons). Such taxa have a number of undesirable properties that distort diversity patterns (see Section 1.2.3. below, and also Sepkoski 1993, 1996b; Foote and Raup 1996; Foote 2000a, b). The use of boundary crossers provides the same result as conventional taxon-counting methods that exclude singletons. Foote (2000a, b) also provided alternative calculation methods for origination and extinction rates normalised for interval length and standing diversity. These are termed *per-capita* rates, and they provide an estimate of the numbers of newly originating or extinct taxa per taxon standing diversity per million years, also known as per *lineage-million-years* (Lmy) (Wei and Kennett 1986; Raup 1985; Foote 1994), i.e. equivalent estimates to those provided by the more familiar per-taxon rates. Foote (2000a) used mathematical modeling techniques to show that per-taxon rates are negatively correlated with interval length and are therefore unreliable. Per-capita rates are based on boundary crossers (See Fig. 1.1) and hence are independent of interval length (Foote 2000a).

1.2.1. Mathematical definitions

This section provides the mathematical definitions and a description of each of the rate estimates outlined above.

Total origination and extinction rates

These provide an estimate of the number of originations and extinctions within an interval, normalised for interval length. Units are taxa per million years.

$$R_s = S / \Delta t \qquad \text{(eq. 1.1)}$$

where:

R_s = Total origination rate

S = Number of originations in interval

Δt = Interval length (change in time t)

$R_e = E / \Delta t$ (eq. 1.2)

where:

R_e = Total extinction rate

E = Number of extinctions in interval

Per-taxon origination and extinction rates

These provide an estimate of the number of originations and extinctions within an interval, normalised for interval length and standing diversity. Units are taxa per Lmy.

$r_s = (S / \Delta t) / D$ (eq. 1.3)

where:

r_s = Per-taxon origination rate

D = Standing diversity of interval

$r_e = (E / \Delta t) / D$ (eq. 1.4)

where:

r_e = Per taxon extinction rate

Per-capita origination and extinction rates

These correspond to Foote's (2000a) rates normalised for interval length and standing diversity. The calculations use boundary crossers (Fig. 1.1A) and are unaffected by interval length. Per-capita rates are simply an alternative to per-taxon rates, both estimate the same metric i.e. the numbers of originations or extinctions occurring during a time unit, per taxon standing diversity, per million years. The use of the logarithm in these equations, and the equation theory, is explained in Figure 1.1B. Units are taxa per Lmy.

$p = -(\ln [N_{bt} / N_t]) / \Delta t$ (eq. 1.5)

where:

p = Per-capita origination rate

N_{bt} = Number of taxa crossing both bottom and top interval boundaries

N_t = Number of taxa crossing top interval boundary

$$q = -(\ln [N_{bt} / N_b]) / \Delta t \qquad \text{(eq. 1.6)}$$

where:

q = Per-capita extinction rate

N_b = Number of taxa crossing bottom interval boundary

The ratio N_{bt} / N_t expresses the proportion of taxa extant at the end of the interval that were already extant at the start, i.e. the proportion of standing diversity *not* originating in the interval. The ratio N_{bt} / N_b expresses the proportion of taxa extant at the start of the interval that survive to the end, i.e. the proportion of standing diversity *not* going extinct in the interval. The logarithm of these ratios decreases linearly with increasing interval time-length. The magnitude of the slope gradient is exactly equal to the origination rate in the first case, and the extinction rate in the second (Fig. 1.1B).

Diversification and turnover rates

The diversification rate is simply origination minus extinction rate. It is a measure of the rate of *net* numbers of new taxa appearing within an interval. Hence it is positive if diversity is increasing, and negative if it is decreasing. Per-capita rates are used here as, unlike per-taxon rates, Foote's (2000a, b) per-capita origination and extinction rates are independent of interval length. The definition of per-capita diversification rate is given below, units are taxa per Lmy.

$$r_d = p - q \qquad \text{(eq. 1.7)}$$

where:

r_d = Rate of diversification

The turnover rate is the sum of origination and extinction rates, and gives an estimate of the number of evolutionary events occurring in an interval. For example, if origination and extinction rates are both high, but equal, diversification rate in an interval is zero, with no diversity change, however turnover rate is high, indicating a dynamic system.

The definition of per-capita diversification rate is given below, units are taxa per Lmy.

$r_t = p + q$ (eq. 1.8)

where:

r_t = Rate of turnover

1.2.2. Measurement methods

The simplest method of obtaining the taxonomic occurrence data required for these diversity and rate calculations is to conduct fieldwork at appropriate outcrop sections. This becomes impractical for larger scale studies of regional or global biodiversity over long time-periods. An alternative method is to obtain occurrence data from primary scientific publications or secondary literature, for example the volumes of the *Treatise on Invertebrate Paleontology* (Moore et al. 1953-2000). Several large compendia of taxonomic occurrence data are currently available, of which two provide global, Phanerozoic coverage of marine animal life (Sepkoski 1992), and of marine and terrestrial life (Benton 1993). Such data sets generally give the stratigraphic intervals of the first and last appearances of taxa, sometimes also with intermediate records, which allows the construction of range information and hence diversity and origination/extinction patterns. For a review of the use of large taxonomic databases see Chapter 3, Section 3.2, and also Benton (1999), and Johnson and McCormick (1999).

1.2.3. Problems with methods

There are a multitude of problems and potential errors and biases inherent in palaeobiodiversity data, in particular associated with the use of large compendia of taxonomic first and last appearances, and stratigraphic dates, to calculate such information. The use of taxonomic databases has been widely criticised (e.g. Hoffman 1985, 1988; Patterson and Smith 1987, 1989; Boucot 1990). Nonetheless they remain the most direct method of addressing many of the 'big questions' of palaeontology (Benton 1999). The concerns associated with biodiversity data and analysis are here divided into taxonomic and sampling/stratigraphic problems.

Taxonomic problems

The ideal taxonomic unit for studying biodiversity patterns is the species. However, it has been estimated that only 1 per cent of all the one-time existing species are ultimately preserved, discovered and described (Raup 1995). Therefore, higher taxonomic ranks, orders, families and genera are often used as proxies for species in large-scale compendia (e.g. Sepkoski 1978, 1979, 1997), in the assumption that the patterns uncovered will reflect the real patterns within species diversity. Some workers have questioned this assumption (e.g. Kitchell and Carr 1985, Flessa and Jablonski 1985, Signor 1985, Benton 1995, 1997, 2001), contending that patterns of diversity plotted at high taxonomic ranks do not necessarily reflect species patterns (see Chapter 3 for a full discussion of this issue).

The reliability of fossil range databases depends upon the expertise of the taxonomist describing and naming the taxa used. In many cases error is introduced due to poor taxonomy (Johnson and McCormick 1999), and the involvement of non-specialists in data compilation (Adrain and Westrop 2000). Errors incorporated into data compilations include over-splitting or lumping together of taxa, the problem of multiple synonyms, and extinctions caused by the re-naming of a taxon emerging from an extinction event, i.e. *pseudoextinctions* (Jeffery 2001). That large data collections include such errors is not in doubt, the question is whether this introduces systematic bias. Studies have shown that diversity curves constructed using independently compiled datasets yield very similar results (Sepkoski et al. 1981; Benton 1995), and that the accumulated knowledge of many years of research has not significantly altered our perceptions of diversity patterns (Sepkoski 1993; Maxwell and Benton 1990), despite a presumed improvement in taxonomic practice. In addition, a direct comparison between trilobite generic diversity patterns constructed using a state-of-the-art dataset compiled by specialists (for description see Westrop and Adrain 1998), and those constructed using a literature-based dataset compiled by a non-specialist (for description see Sepkoski 1996b) produced very similar results, despite the large numbers of systematic and stratigraphic errors in the latter (Adrain and Westrop 2000).

Potentially more serious are the large numbers of non-monophyletic groups within the taxonomic literature. Smith and Patterson (1988) reviewed the status of post-Palaeozoic echinoderm and fish families from Sepkoski's (1992) data set and found that only 33% were monophyletic, the rest were paraphyletic, polyphyletic, monotypic or of uncertain status. From a strictly cladistic viewpoint only monophyletic groups have a

biological reality (Smith 1994). Paraphyletic taxa, due to the supposed arbitrary nature of their definition, may distort diversity patterns with pseudo-originations and extinctions, and it has been claimed that a true picture of life's diversification can only be gained with the sole use of monophyletic clades, achieved through the cladistic method of taxonomy (Patterson and Smith 1987; Smith and Patterson 1988). A recent re-analysis of the response of heart urchins (Atelostomate echinoids) to the Cretaceous-Tertiary extinction event demonstrated that previous estimates of taxonomic losses within this group were far too high due to paraphyly and other taxonomic errors (Jeffery 2001). The distorting effect of paraphyletic taxa has been challenged both with gastropod fossil data (Wagner 1995), and computer simulations (Sepkoski and Kendrick 1993) which argued that taxonomic datasets including paraphyletic taxa adequately capture the underlying pattern of species diversity under a variety of diversification conditions. Robeck et al. (2000) suggested that the monophyletic vs. paraphyletic argument may be misplaced, and proposed that the best approach to diversity analysis is to use a mixture of taxonomic ranks, so as to match most closely the inferred quality of the fossil sample. Nonetheless, it is an ongoing aim for those who construct taxonomic datasets to refine their data and ensure that the taxa contained within are monophyletic and cladistically robust.

Sampling and stratigraphic problems

The fossil record does not provide an even and unbiased sample of past life. It is incomplete by a variety of measures, including *organismic* incompleteness, the failure of most organisms to fossilize, and *stratigraphic* incompleteness, gaps in rock sequences representing unpreserved segments of time (Kemp 1999). There is a strong bias in the fossil record towards preservation of organisms with hard skeletal elements as opposed to the soft bodied elements that make up the majority of the biomass. A similar bias is apparent towards marine and lacustrine faunas, which are more easily preserved than terrestrial organisms, leading to the assumption that the continental fossil record is poorer than the marine (Wagner 2000), and less useful for biodiversity analysis. Another organismic effect is the influence of the extant fauna on diversity patterns. Termed the *Pull of the Recent* (Raup 1979a), this occurs because the far greater sample of life in the modern biota, as compared to the fossil record, pulls the ranges of their fossil representatives forward in time, and therefore inflates Cenozoic biodiversity counts. Despite this artefact, a large Cenozoic rise in diversity is a robust feature of

Phanerozoic diversity patterns, even when Recent taxa are included only if they have a Plio-Pleistocene fossil record (Sepkoski 1997).

Stratigraphic incompleteness is an obvious concern for palaeontologists, particularly those interested in biodiversity patterns. Several recent studies have found a correlation between the perceived patterns of taxonomic occurrences, and the amount of rock outcrop available for sampling (Smith et al. 2001; Peters and Foote 2001, 2002), suggesting that biodiversity patterns may be an artefact of the rock record and not a real signal. However, the results of these studies are also consistent with the possibility that a common geological cause, the most obvious example being sea-level change, drives both patterns of diversification and the amount of sedimentary rock laid down (Peters and Foote 2002). It is also probable that while the quantity of rock volume may have a strong influence on short-term diversity patterns, it cannot adequately explain the long-term signal apparent in biodiversity data (Foote, pers. comm.), despite the fact that there is progressively less rock exposed going back through time. Two further problems are associated with stratigraphic incompleteness, both of which introduce noise and skew to the perceived patterns. Firstly is the matter of taxa known from only a single stratigraphic interval, also known as 'singletons'. Such taxa introduce more noise than signal to the data for a variety of reasons (Sepkoski 1996b): (1) they are often rare taxa and their presence indicates an increase in sampling intensity rather than diversity; (2) the number of singletons is highly correlated with stage duration and their relative frequency is affected disproportionately by incomplete preservation; and (3) it is probable that many singletons are actually synonyms of other taxa. Therefore, it is generally desirable to remove singletons from large compendia of diversity data (Sepkoski 1993; Foote and Raup 1996) or to use 'boundary crosser' measurements of diversity that naturally exclude taxa that occur in only one interval (Alroy 1998, 1999; Bambach 1999; Foote 2000a, b).

The second potential source of skew within diversity data is the fact that first and last appearances of taxa in the fossil record rarely represent their true origination and extinction points in time (Novacek & Norell 1982; Smith 1994; Sepkoski 1996b). Last appearance times invariably fall within intervals preceding the true extinction times of taxa and, when many extinctions occur contemporaneously, the combined effect smears the event backwards in time. This is known as the Signor-Lipps effect (Signor and Lipps 1982). There is a comparable situation for first appearances, where radiation events are smeared forwards in time. Similar artefacts occur towards the start and end of

periods used in diversity analysis, produced by the decreasing probability of finding earlier or later taxonomic occurrences as the boundaries are approached. These are termed *edge-effects* by Foote (2000a).

Recently, two methods of 'enhancing' diversity counts have been developed in an attempt to correct for incomplete sampling. The first, termed the *phylogenetic method* of estimating biodiversity (Smith 1994) uses the phylogenetic relationships between taxa to alter first appearance times, and hence increase taxonomic ranges and diversity counts (e.g. Novacek & Norell 1982; Norell & Novacek 1992a, 1992b; Smith 1988). Such range extensions have been termed *ghost lineages* (Norell 1992, 1993). It has been predicted that there is an inherent bias involved in only correcting the first appearance times of taxa (Wagner 2000), resulting in skew within the diversity patterns. For a full discussion of the phylogenetic method of estimating diversity see Chapter 2.
A second method of altering raw diversity data to correct for preservation and collection sampling bias is derived from rarefaction techniques (Raup 1975), which have previously been applied as a sampling normalisation (Miller and Foote 1996). Alroy (1999, 2000) has developed the concept further into a method for standardising sampling in successive time intervals. The procedure involves the compilation of detailed faunal lists for many localities within the time period of interest. A number of faunal lists are then drawn at random for each interval until a predetermined total is reached; all intervals must be able to reach this total. Hence, an identical number of samples is drawn for each interval. From this random sample, diversity and rates data are calculated. The procedure is repeated at least 100 times and averages computed to give the final diversity and rates values. The method is termed *sampling standardization* (Alroy et al. 2000). Preliminary results from a new database designed for this technique indicate that global marine diversity may have reached an early plateau in the Ordovician, since when there has been little further diversification (Alroy et al. 2001). However, this database still provides low coverage of the time periods, geographic area and taxonomic groups included. Sampling standardization cannot be used with the currently available large global taxonomic compendia (e.g. Sepkoski 1992; Benton 1993) as locality faunal lists are required rather than simply global first and last appearances. Finally, the sampling standardization technique works by reducing the numbers of samples within every time interval down to the level of the lowest, and hence information is lost. The resulting diversity counts can be seen as minimum estimates.

A common element of these methods is the introduction of assumptions that distort the raw pattern of biodiversity provided by the fossil record. While the fossil record is undoubtedly incomplete and patchy, the question is one of the *scale* of investigation for which the data are used. In the field many stratigraphic sections and localities have a paucity of fossils, contain sedimentary gaps and are certainly incomplete. On a global scale, however, our accumulated knowledge of taxonomic ranges using units of stages or epochs is good enough to recover long-term evolutionary patterns (Benton 2001). The term *adequacy* (Paul 1990) has been coined to describe the level of completeness of the fossil record required for different scales of analysis. Several studies have indicated that the fossil record is adequate for recovering global Phanerozoic biodiversity patterns. These include analyses of the continental fossil record (Benton and Hitchin 1996; Benton et al. 1999), the completeness of dominant classes of marine animals (Foote and Sepkoski 1999), and the quality of the fossil record through time as assessed by congruence between cladogram shape and the sequence of fossils in the rocks (Benton et al. 2000), and by comparisons of the quality of exceptional fossil assemblages through time (Allison and Briggs 1993).

1.3. Models of biodiversity

Despite the perceived problems with palaeobiodiversity analysis, this area of research has been one of expanding activity and progress over the past twenty-five years (Miller 2000). A major theme of such activity has been the search for generalised models of biodiversification, describing both patterns and processes through time, which can be universally applied to data over a variety of scales, up to the level of Phanerozoic global diversity dynamics (e.g. papers in Valentine 1985; Raup and Jablonski 1986; McKinney and Drake 1998; Erwin and Wing 2000). The anticipated outcome of such theories is the formulation of a simple, universal model of biodiversification that describes the patterns apparent from empirical data, but also encompasses the ecological processes governing the myriad causes of individual species originations and extinctions. The validity of such an endeavour has been questioned (Miller 2000) but the results of this activity have provided some of the most widely cited and debated theories of recent palaeontological research. In the following sections are described the two most prominent models of biodiversification through time.

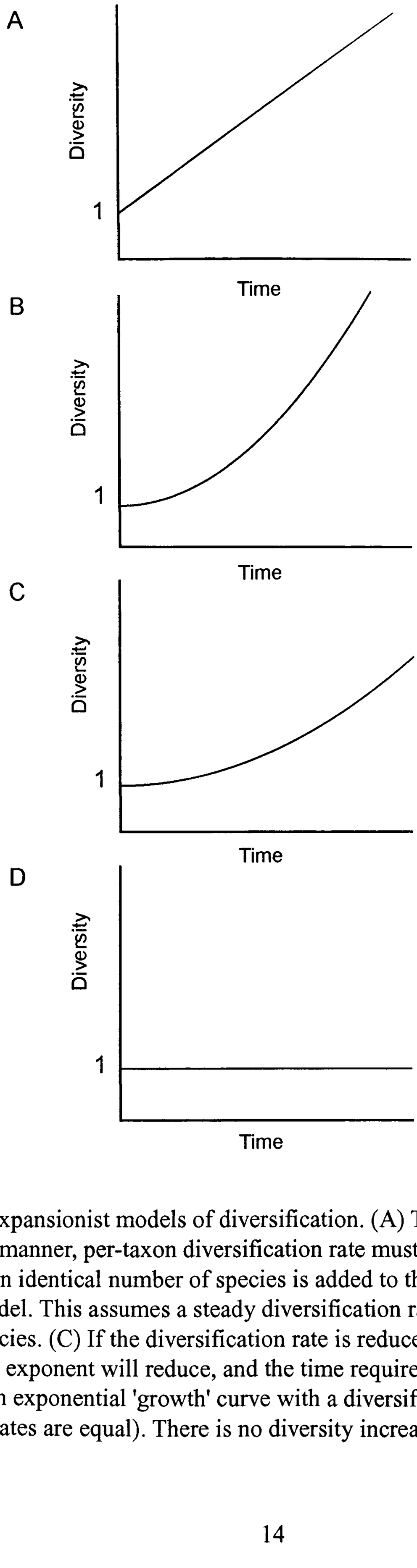


FIGURE 1.2. Expansionist models of diversification. (A) The additive model. For diversity to increase in this manner, per-taxon diversification rate must decrease with time at a constant rate, such that an identical number of species is added to the system per unit time. (B) The exponential model. This assumes a steady diversification rate through time, hence a constant doubling of species. (C) If the diversification rate is reduced, e.g. by an increase in extinction rate, the growth exponent will reduce, and the time required for a doubling of diversity will increase. (D) An exponential 'growth' curve with a diversification rate of zero (i.e. origination and extinction rates are equal). There is no diversity increase in the system.

1.3.1. Non-equilibrium models

The evolution of life is a multiplicative process (Sepkoski 1996a). An exponential growth curve – a constant doubling of individuals through time, is the normal expectation of a reproductive community of organisms with no constraints placed upon their numbers. Speciation can also be seen as an exponential process in that it is the splitting of lineages from one to two, from two to four, etc. (Benton 2001). This of course is based on speciation by cladogenesis, as opposed to anagenesis in which no increase in species numbers is implied. Models of continuous increase in species number have been termed *expansion* or *non-equilibrium* models (Benton 2001) and all expect a constant mean diversification rate where no diversity equilibrium is reached. The simplest expansion model is based on a simple exponential growth curve, here termed the *exponential model*. Another growth form which could be applied to diversification is a linear increase, or *additive* model, where a fixed number of new species is added to a diversity system with each unit of time (Fig. 1.2A). This, however, is difficult to explain in terms of an evolutionary branching process as it implies an accelerating extinction rate, and/or a decelerating origination rate, so that the net outcome is exactly the same number of new species per unit time (Benton 1997). Due to this, the additive model is not well supported.

1.3.1.1. Mathematical definition of the exponential model

The exponential model is a growth curve with a constant doubling of species, or higher taxa, through time. Change in diversity through time (Sepkoski 1978) is defined as:

$$\Delta D / \Delta t = r_d D \qquad \text{(eq. 1.9)}$$

where:

D = standing diversity

t = time

r_d = rate of diversification (per lineage million years), i.e. origination – extinction rate.

This equation, written as a differential and integrated, gives diversity as a function of time (Sepkoski 1978):

$$D = D_0.\exp(r_d t) \qquad \text{(eq. 1.10)}$$

where:

D_0 = Initial diversity level at time $t = 0$.

At its simplest, this model incorporates a non-changing, positive rate of diversification, resulting in continuously increasing diversity (Fig. 1.2B). If there is no extinction, the form of the exponential is governed by the origination rate. With extinction the exponent is lowered, and the time required for diversity doubling increases (Fig. 1.2C), unless origination rate also increases. It is the difference between the two, the diversification rate r_d, that is the defining parameter controlling growth rate. If the rate of origination equals that of extinction, the diversification rate is zero and hence, from equation 1.10 above, diversity D through time remains constant at the initial diversity level D_0 (Fig. 1.2D). However, it is generally assumed that diversity within evolutionary systems grows initially and an exponential model with a diversification rate parameter of zero is therefore unrealistic.

The term *damped exponential* is a confusing one that has been used to describe two different concepts. Firstly, it has been applied to an exponential diversification curve where the exponent is not produced exclusively by unfettered origination under unconstrained conditions. Extinction rate is included which results in a lower diversification rate parameter (Benton 2001), and hence an increased amount of time required for doubling of diversity to take place. Such 'damped' diversification of a group could be caused by many factors, including competition with other diversifying taxa and environmental perturbations. Secondly, the term *damped exponential* has been used to describe the gradual departure from exponential during the initial growth stage of a logistic curve before the equilibrium period is reached (Benton 2001), for example that used to model bivalve diversification (Miller and Sepkoski 1988; Sepkoski 1996a), which is an exponential curve. In mathematical terms, 'damping' is more appropriately applied to this second concept, i.e. the addition of an extra parameter to the exponential equation, which curbs growth over time (i.e. a logistic equation), rather than changing the exponential term itself, which alters the slope of the curve from the outset.

Here, only the term *exponential model* is used, defined by the possession of a sole free parameter, r_d, governing the acceleration of the growth curve, as opposed to the *logistic model* which has two free parameters governing its form, r_d, and a damping term, D_{eq} - the equilibrium parameter (see section 1.3.2.1 below). The exponential parameter r_d can of course be affected by the presence or absence of competitors; the exponential model does not preclude competition. However it does not predetermine an upper limit to diversity. Empirical patterns of Phanerozoic familial terrestrial life, and 'all life', have been interpreted as conforming to the exponential model (Benton 1995, 1997).

1.3.2. Equilibrium models

Equilibrium models of biodiversification assume that there are limits to the numbers of species and higher taxa sustainable by the Earth, limits that have been reached in the past and will be reached in the future. Diversity is modeled not as continuous growth, but as a series of short radiation periods interspersed with long periods of stability when taxonomic diversity does not change significantly. These equilibrium periods are terminated by a mass extinction event, which alters the diversity dynamics of the system and allows a new period of radiation to commence. The best developed of these models is that proposed in a series of papers by Sepkoski (1978, 1979, 1984), and named the *kinetic model* of Phanerozoic taxonomic diversity. It is termed the *logistic model* here to describe its shape. The theory for the logistic model was borrowed from the concepts of *island biogeography* (MacArthur and Wilson 1967), but in effect regarding the whole world as an island (see Section 1.3.3). The model expresses diversification as a logistic process, with an early exponential rise followed by a long 'plateau' in taxonomic diversity, a period when diversity fluctuates around an equilibrium level – hence the term 'kinetic'. An empirical diversity curve for marine orders seemed to fit this model well (Sepkoski 1978 and Fig. 1.3A, B), and it also fitted with Raup's (1972) earlier predictions that species diversity through the Phanerozoic increased dramatically in the Cambro-Ordovician, with little subsequent growth for the remainder of the Phanerozoic. Such a single, long diversity equilibrium is also hinted at in recent attempts to uncover the pattern of generic marine Phanerozoic biodiversity using sampling standardisation techniques (Alroy et al. 2000).

When Sepkoski (1979, 1984) constructed a similar curve using his extensive compilation of marine fossil families the situation was much more complex than for orders. Instead of one early radiation followed by a long equilibrium, marine family diversity increased throughout the Phanerozoic in a series of apparently distinct stages. This apparent pattern was similar to those revealed by several independently compiled datasets (Sepkoski et al. 1981), and was interpreted as displaying three phases of diversification, each consisting of a logistic rise and then plateau in diversity, complying with Bambach's (1977) recognition of 'multiple equilibria' in his species richness data through the Phanerozoic. Furthermore, Sepkoski elaborated on previous work by Flessa and Imbrie (1973) on the concept of *evolutionary faunas*. He performed a factor analysis on marine familial data, grouping classes with similar diversity patterns into three diversity associations which he termed the Cambrian, Palaeozoic and Modern faunas (Sepkoski 1981; Sepkoski and Miller 1985). Each fauna consisted of distinct classes of marine animals, predominantly trilobites in the Cambrian, articulate brachiopods in the Palaeozoic, and bivalves and gastropods in the Modern, which successively replaced each other. The waxing and waning of these faunas was interpreted by Sepkoski as largely determining the empirical pattern seen at familial level (Fig. 1.3C), and the simple logistic model was extended to describe the pattern as multiple logistic curves, so that each fauna or 'phase' interacted with the other two (Fig. 1.3D). This was termed the *three-phase kinetic model* (Sepkoski 1984), and consisted of coupled logistic equations with parameters dependent upon the state of the diversity system of other co-existing phases. The model was further refined by adding the capacity to include *diversity perturbations* or extinction events within the system (Fig. 1.3E) and forms of this model have been applied to the diversification dynamics of Phanerozoic marine life (Sepkoski 1984; Courtillot and Gaudemer 1996), brachiopod and bivalve diversification (Miller and Sepkoski 1988; Sepkoski 1996a) and cheilostome and cyclostome bryozoan diversification (Sepkoski et al. 2000). However, the three faunas may be criticised as being post-hoc statistical constructs, each of which contains a mixture of taxonomic ranks.

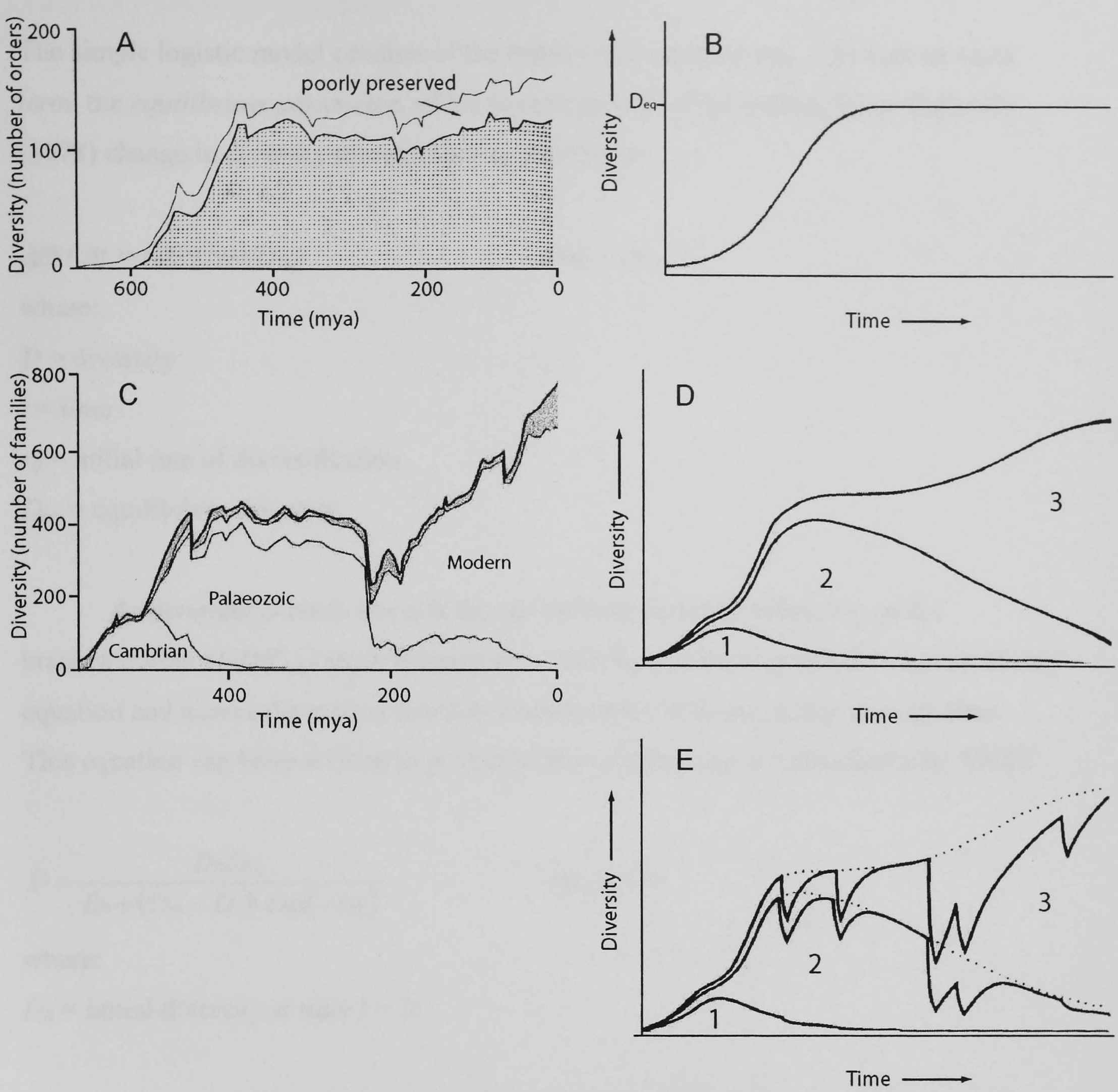


FIGURE 1.3. Empirical and logistic model Phanerozoic marine diversity curves. (A) Marine orders (After Sepkoski 1978). (B) A solution of the simple logistic model (after Sepkoski 1978). D_{eq} indicates the value of the equilibrium parameter. (C) Marine familial curve incorporating the diversity trajectories of the three 'evolutionary faunas' (after Sepkoski 1984). (D) Solutions of the multiple-phase logistic model equations, the numbers indicate each phase (after Sepkoski 1984). (E) Solutions of the multiple-phase logistic model equations, with five mass extinctions incorporated (after Sepkoski 1984).

1.3.2.1. Mathematical definitions of the logistic model

The simple logistic model consists of the exponential equation (eq. 1.9) with an extra term, the *equilibrium parameter*, added to curb growth of the system. From Sepkoski (1978) change in diversity through time is defined as:

$$\Delta D / \Delta t = r_0 D\,(1\text{-}D/D_{eq}) \qquad \text{(eq. 1.11)}$$

where:

D = diversity

t = time

r_0 = initial rate of diversification

D_{eq} = equilibrium diversity

As diversity D tends towards the equilibrium diversity value D_{eq}, so the bracketed term $(1\text{-}D/D_{eq})$ tends towards zero. This damps the exponential element of the equation and moves the system towards a steady-state, with no change through time. This equation can be re-written to give diversity as a function of time (Sepkoski 1978):

$$D = \frac{D_0 D_{eq}}{D_0 + (D_{eq} - D_0)\cdot \exp(-r_0 t)} \qquad \text{(eq. 1.12)}$$

where:

D_0 = initial diversity at time $t = 0$.

The value of the equilibrium diversity, D_{eq}, is defined using Sepkoski's (1978) models for the diversity-dependent behaviour of per-taxon origination and extinction rates with increasing standing diversity within a system. These are simply linear functions:

$$r_s = k_s - aD \qquad \text{(eq. 1.13)}$$

$$r_e = k_e + bD \qquad \text{(eq. 1.14)}$$

where:

r_s = per-taxon rate of origination

r_e = per-taxon rate of extinction

k_s = initial rate of origination

k_e = initial rate of extinction

a and b are constants representing the slopes of the functions (Fig. 1.4B).

The origination rate model has a negative slope as, according to the predictions of diversity-dependence, the rate of new taxonomic appearances decreases with increasing diversity due to crowding effects (Sepkoski 1978, 1979). The opposite is the case for extinction rate, which increases as taxonomic crowding increases. Thus the rate of diversity increase within the system slows and eventually halts at the equilibrium value. This value is set as the intersection of the two rate functions (Fig. 1.4B) and is defined as:

$$D_{eq} = \frac{k_s - k_e}{a + b} \qquad \text{(eq. 1.15).}$$

Hence, through the equilibrium parameter D_{eq}, the logistic model presets an upper limit to diversity in the system being modelled.

Diversity-dependent models for the behaviour of *total* origination and extinction rates with increasing diversity are simply the first-order per-taxon rate models multiplied through by standing diversity (Sepkoski 1978). This gives second-order, parabolic functions:

$$R_s = k_s D - aD^2 \qquad \text{(eq. 1.16)}$$

$$R_e = k_e D + bD^2 \qquad \text{(eq. 1.17)}$$

where:

R_s = Total origination rate

R_e = Total extinction rate.

Figure 1.4C shows the expected form of these models leading up to a period of equilibrium.

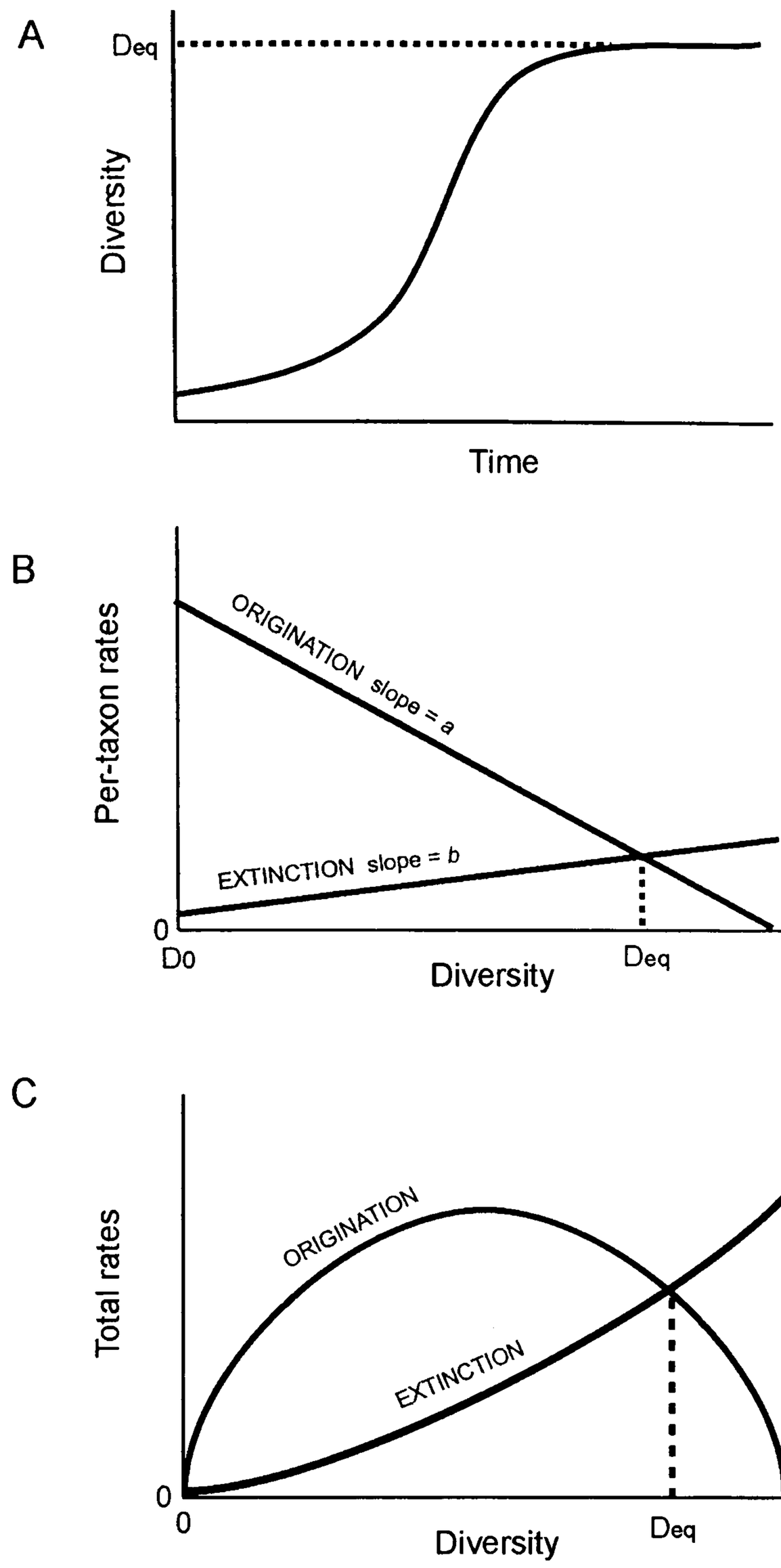


FIGURE 1.4. Predictions of the logistic model of biodiversification. (A) A logistic growth pattern consists of an initial exponential rise, followed by a gradual decrease and then cessation of diversification, producing an equilibrium period at a diversity level D_{eq}. (B) The kinetic model states that logistic growth will be produced by diversity-dependent origination and extincton rates. Models for the change in per-taxon rates with increasing diversity predict that the slopes of the two functions, *a* and *b* in eq. 1.13 and 1.14, intersect at the diversity equilibrium (after Sepkoski 1978). (C) The models for the change in total rates with increasing diversity take the form of parabolic functions intersecting at the equilibrium diversity value (after Sepkoski 1978).

The more complex equation for the three-phase logistic model of diversification (from Sepkoski 1984) is given below:

$$dD_i / dt = r_{0i} D_i (1 - \sum_j D_j / D_{ieq}) \qquad \text{(eq. 1.18)}$$

where:

i = Represents the individual phase (or evolutionary fauna)

j = Represents all three phases combined

D_i = Diversity of the ith phase

r_{0i} = Initial diversification rate of the ith phase

D_{ieq} = Equilibrium diversity of the ith phase

$\sum_j D_j$ = summed diversity of all three phases in the system.

Two or more solutions to this equation can be created, termed 'coupled logistic equations', which will model interacting 'phases', faunas or taxa, within one diversity system. Solutions of this model for three diversity phases were presented by Sepkoski (1984), and given what he termed an 'eyeballed' fit to familial diversity data for the three evolutionary faunas. The resulting correlation coefficients were high suggesting a good fit of the multiple-phase model to the empirical data. Sepkoski (1979, Fig. 10) also provided solutions of the total origination and extinction rate models for a two-phase system, but these coupled equations were not fitted to the empirical data due to technical problems associated with higher order least-squares fits (Sepkoski 1979). Instead, the single phase total rates models (eqs. 1.16, 1.17) were applied to both Cambrian data, and later Palaeozoic familial rate data, plotted against diversity. The stratigraphic intervals used were Cambrian stages and post-Cambrian series. A good fit was found for the origination rate data through the post-Cambrian Palaeozoic, but only a poor fit for extinction rate (Sepkoski 1979).

1.3.3. Ecological-evolutionary basis for the models

Exponential model

The exponential model assumes constant growth in a system, even if such growth is relatively slow (e.g. Fig. 1.2C). Equilibrium models of diversification are based on ecological species-area theories (See Section 1.3.2.2. below). Evolution through time, however, adds a dimension to short-term expansion of diversity in a fixed area – namely the possibility of evolutionary innovation, new adaptive features of organisms that allow the exploitation of new areas of ecospace and hence raise diversity (Whittaker 1977; Benton 1995, 1997). Indeed diversification events drive new originations themselves, providing novel opportunities and niches for exploitation (Kirchner and Weil 2000a), and evolutionary 'arms races' produce a concept known as escalation (Vermeij 1987) in which the appearance of adaptations for predation are correlated with those for escape and defence in prey species. Such innovations include the growth of hard skeletons and burrowing in the marine realm, and terrestrialisation and flight among continental organisms. Ausich and Bottjer (1982, 1985) proposed the theory of diversity increase by *tiering*, i.e. the extent to which the vertical dimension of a habitat is utilised. For example, most Palaeozoic taxa were epifaunal, but the Mesozoic and Cenozoic saw an increase in the numbers of infaunal organisms, and in the depths to which they burrow. There is no reason to assume that the ability of species to innovate is slowing down, in fact quite the opposite. The biosphere has also changed over time. It has been shown that the number of geographically distinct areas in the marine realm capable of supporting a diverse ecosystem is positively correlated with increasing diversity through the Phanerozoic (Signor 1990).

Logistic model

The logistic model of biodiversification is based upon the classic ecological theories of species-area effect and inter-species competition. The species-area effect simply states that the larger the area of available habitat, the greater is the number of species that will be found within it (Begon et al. 1990). This was scaled-up to reasonably large areas of land by MacArthur and Wilson (1967), who formulated their *theory of island biogeography*, explaining how distance and area combine to regulate the balance between species immigration and extinction in island populations. Underpinning the species-area effect is classic competition theory, mathematically described by the

Lotka-Volterra equations (Fig. 1.5A), in which two co-existing species within a closed system compete with each other for resources, and their population sizes grow logistically as a result. The rate of expansion of each population is determined by the species reproductive rate and the population size of the competing species. Eventually, either a dynamic equilibrium is reached, determined by the availability of resources in the system, or one species excludes the other (Fig. 1.5B).

These ecological theories have been scaled up to become macroevolutionary concepts. Sepkoski's (1978) kinetic model and diversity-dependent equations for per-taxon origination and extinction rates are simply adaptations of the Lotka-Volterra equations governing population growth. In the same way, the concept of an ecological *carrying-capacity*, or upper limit to species numbers, has been applied to the diversity system of the Earth. The carrying-capacity defines the number of *niches*, opportunities available for exploitation by existing and newly evolving species, within an ecosystem. Equilibrium theories predict that such niches are finite in number, hence Darwin's (1859) analogy of the field of wedges, where an originating taxon can only exploit a niche by ousting another already utilising it - one wedge being driven into the field and forcing out another. Vermeij (1995) suggested that diversification is controlled by resource provision, with radiation periods such as that of the Cambro-Ordovician produced by a increasing supply of raw materials and energy to the system. Reductions in productivity reinforce adaptational constraints and bring about extinctions and the slowing of diversification. Vermeij saw the intensification of competition as being key to maintaining the status-quo in a diversity system, as extreme phenotypes are pruned and further evolution is prevented. A taxonomic carrying-capacity maintained by inter-taxon competition is the mechanism proposed to produce the logistic shape of diversification patterns (Miller and Sepkoski 1988; Sepkoski 1996a). Sepkoski (1979, 1997) pointed out that it is unrealistic to expect continued diversity expansion throughout the Phanerozoic at the same rate as that seen in the Cambrian diversity explosion, and cited the accelerated diversification rates of many taxa after mass extinction events as evidence for diversity-damping and inter-taxonomic competition (Sepkoski 1998a). It could also be the case that a progressively increasing global carrying capacity is produced by increased tiering and other ecological innovations. Conversely, Benton (1997), while recognising an ultimate limit to the number of taxa that can inhabit the Earth, argued that until this limit is reached, evolutionary innovations are enough to transcend the damping effect of competition, and to keep the

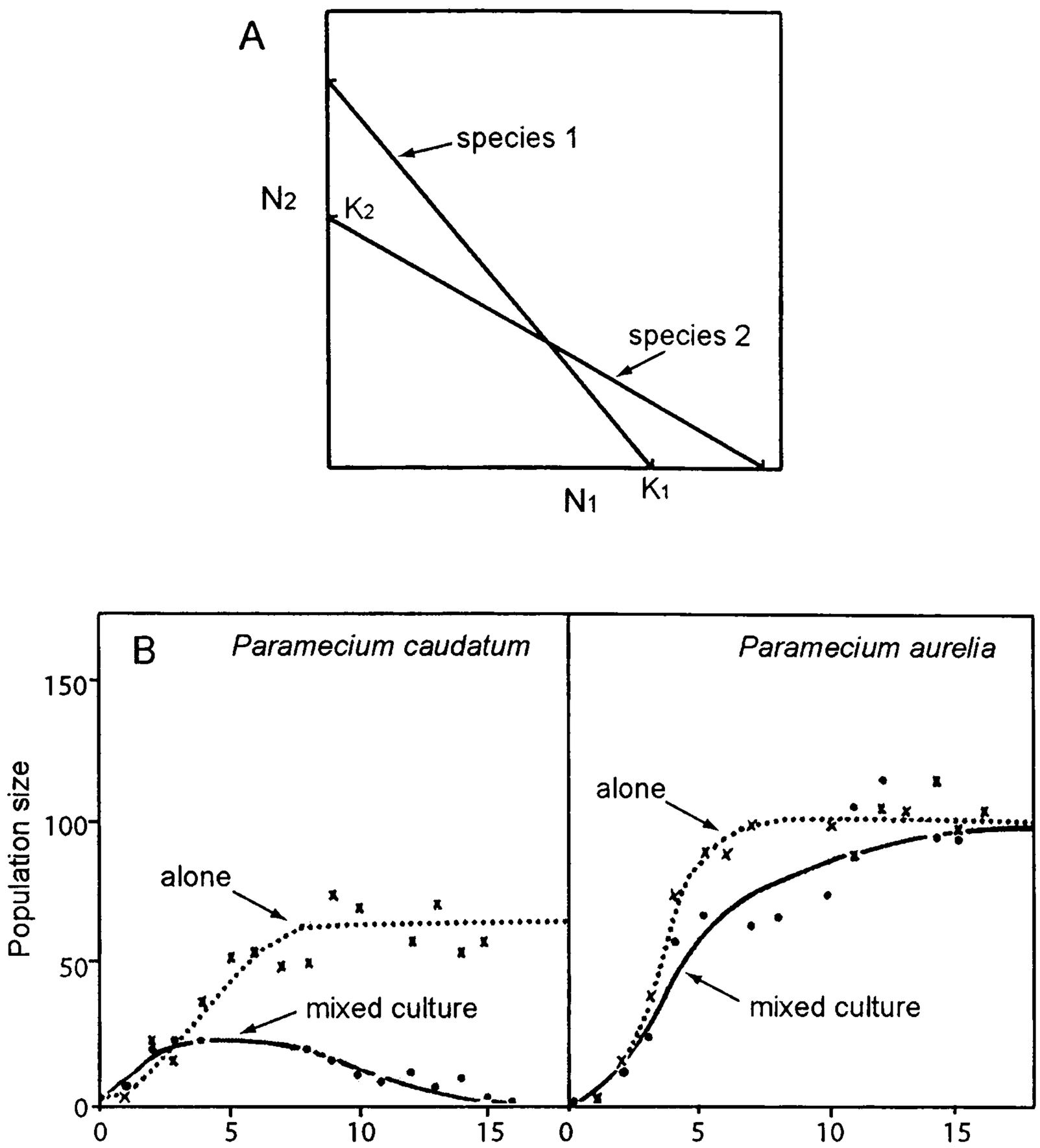


FIGURE 1.5. Competition between two populations of coexisting species. (A) Competitive equilibrium. An equilibrium solution of the Lotka-Volterra equations describing inter-species competition. *N* indicates the population sizes of species 1 and 2. *K* is the environmental carrying capacity for each species in the absence of the other. The lines represent the declining numbers of each species with increasing population size of the other, and the slopes equal the competition coefficients of the equations. A stable equilibrium is achieved where the two lines intersect, at which point the population of each species is maintained below its carrying capacity (after Sepkoski 1996). (B) Competitive exclusion. Experimental results of competition between two species of the protist *Paramecium*. The dotted lines indicate the growth of the named species in isolation, the bold lines are growth of the species when in a mixed culture with the other. When grown together, species *P. aurelia* out-competes and excludes *P. caudatum* in approximately 15 days (after Gause 1934).

trajectory of diversification upwards. Both the exponential and logistic models are flexible enough to allow for periods of diversity increase, and of inter-taxonomic competition. Both can be tested by application to empirical data sets, and their defining parameters estimated. In this way the predictions of both regarding the reality or otherwise of diversity-dependent turnover rates and equilibrium periods can be investigated.

1.4. The Palaeozoic plateau as evidence for equilibrium models

The strongest evidence for equilibrium models of biodiversification is the *Palaeozoic plateau* in marine diversity curves (Benton 1997), i.e. the period from the Mid-Ordovician to the Mid-Permian, during which global marine familial diversity appears to remain constant (Fig. 1.6), with fluctuations around the mean level (Sepkoski 1979, 1984, 1997; Sepkoski et al. 1981; Benton 1995). Drops in diversity are matched by subsequent rises, and vice versa, so maintaining an equilibrium. Such apparently diversity-dependent behaviour of originations and extinctions is a key prediction of the logistic model. No other long-term global equilibria are apparent in the fossil record.

The proposed Cambrian equilibrium in marine diversity (Sepkoski 1979, 1984) is relatively short, and its expression depends greatly upon the number of stratigraphic intervals used, and the exclusion of taxa with uncertain ranges such as basal brachiopods, arthropods and other problematica (Benton 1995), and over-split taxa such as the archaeocyathids (Sepkoski 1979). The 'third-phase' of the kinetic model at the family level shows little sign of reaching the predicted plateau. Global diversification curves for continental life and 'all-life' (Benton 1993), do not display a long-term equilibrium like the marine Palaeozoic plateau – indeed the curve for continental life appears exponential (Benton 1995, 1997, 2001). Hence, the plateau remains the most compelling direct evidence for the equilibrium theories of biodiversification.

1.4.1. Three alternative hypotheses for the plateau

Benton (1995) listed three interpretations of the Palaeozoic plateau, two of which assumed that the plateau is real, and either maintained at, or below a global carrying capacity. The third suggested that the plateau is not real, but an artefact of the familial

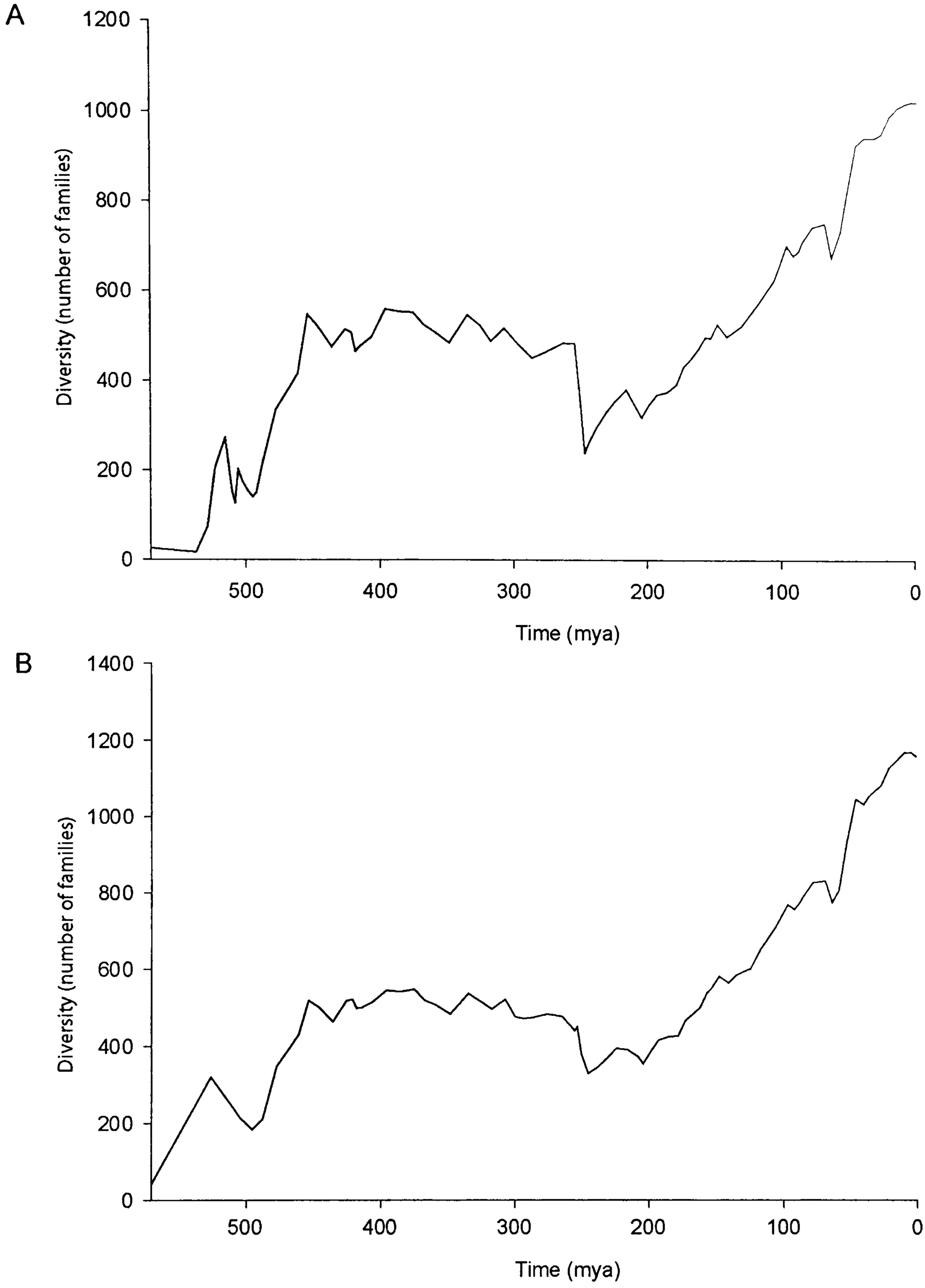


FIGURE 1.6. The Palaeozoic plateau in marine familial diversity. Two independently compiled, global Phanerozoic data sets clearly show the apparent halt in diversification of marine life from the end of the Ordovician radiations (approx. 450 mya) continuing through until the Permian extinction event (approx. 250 mya). (A) Marine familial diversity through the Phanerozoic, raw data from Sepkoski (1992). (B) Marine familial diversity through the Phanerozoic, raw data from Benton (1993).

level data used to plot the curve. This theme is developed here, and the following three hypotheses of the plateau are proposed:

1) The plateau is real, and is an ecologically determined structure. This view complies with the predictions of the logistic and other equilibrium models: there are global carrying-capacities which limit diversity in the world's oceans, and which have periodically been reached in the past, or at least approached while diversity is maintained below the carrying-capacity by environmental perturbations. According to this model origination rate or extinction rate, or both, display diversity-dependence – the rate determined by crowding effects and inter-taxonomic competition.
2) The plateau is real, but is a stochastic structure. This is the *neutral model* of Hoffman (1986, 1989) which assumes random rates of origination and extinction. No ecological or biologically determined constraints are implied, and the apparent equilibrium with fluctuations is simply a random element in the growth pattern of diversity.
3) The plateau is an artefact of taxonomic level. This viewpoint was advocated by Benton (1997, 2001) who presented empirical and model data curves for marine diversity at ordinal, familial, generic and species-level, and suggested that the logistic pattern of the plateau decays into an exponential curve as the taxonomic hierarchy is descended.

1.4.2. Aims of this research

The above three interpretations of the Palaeozoic plateau are considered and evidence for each hypothesis sought. Palaeozoic biodiversity patterns are analysed comprehensively using the most up-to-date compendia of global Phanerozoic taxonomic-range data available. This includes the application of model-fitting techniques and computer simulations. In addition, the phylogenetic method of enhancing diversity counts is tested using simulated data sets. The aim of this research is to determine which interpretation of the plateau is the most probable, and what significance this has for mathematical modeling of global biodiversity through time.

CHAPTER 2. ESTIMATING PALAEODIVERSITIES – A TEST OF THE PHYLOGENETIC METHOD

2.1. Introduction

Investigations into the patterns of ancient biodiversity are often concerned with uncovering the diversification history of a particular group through a particular time period. The group can range in size from a single family in a specific location, up to the clade of all life found globally, and time periods can range from tens of thousands of years up to hundreds of millions of years (e.g. Valentine 1969; Raup 1972; Sepkoski 1984). However the method of uncovering their diversification patterns has traditionally been the same. Some level in the taxonomic hierarchy is selected and the earliest and latest records of any member species are used to define the total geological range of the higher taxon. The numbers of taxa present within a sequence of time intervals are then summed to produce a series of diversity counts that are used to determine the overall pattern. This reliance on the observed stratigraphic occurrence of taxa has been termed the 'taxic' (Levinton 1988) or 'taxon counting' approach.

2.1.1. The 'taxic' versus the 'phylogenetic' approach to diversity estimates

Since Phillips (1860) first investigated patterns of ancient biodiversity as recorded in the fossil record, the method of compiling diversity counts has invariably been the taxic approach (see Chapter 1, Section 1.2). More recently this direct reading of the history of life from stratigraphy has come under increasing fire for its reliance on what is perceived as an incomplete and biased sample as represented by the fossil record (e.g. Novacek & Norell 1982; Norell & Novacek 1992a, 1992b; Smith 1988). Various methods of solving the problems associated with the incompleteness of the fossil record have been tried to enhance the simple taxon counting method of estimating diversity, including idealised sampling theory to estimate how much of a taxon's range is unsampled (e.g. Signor and Lipps 1982; Strauss and Sadler 1989; Marshall 1990, 1991) and standardisation techniques to correct for differences in taxon sampling rate across time intervals (e.g. Raup 1975; Miller and Foote 1996; Alroy 2000, Alroy et al. 2001). A third method, which has grown out of the increasing use of cladistics to determine phylogeny, is termed the *phylogenetic* approach (Smith 1994). This uses the

relationships between taxa as recovered by cladistic analysis and calibrated by stratigraphy, to predict the maximum age of divergence of sister groups. It also provides a minimum estimate of unsampled range prior to first appearance of the taxa in the fossil record. This unsampled range has been termed the 'ghost lineage' (Norell 1993).

The principle of using the relationships between taxa to identify gaps in the fossil record was first explicitly noted by Shaw (1964). Methods of calculating ghost lineages and using them to enhance diversity estimates were outlined by Fisher (1982) and Paul (1982) and first used by Smith (1982). Recently a more detailed set of methods has been proposed by Norell (1992, 1993) suggesting that the application of cladistics to patterns of biodiversity offers an alternative and superior history of life than that obtained by direct reading of the rock record. The result is a taxic history predicted by phylogeny and not always in accordance with the stratigraphic occurrence of fossils (e.g. Smith 1988).

2.1.2. Overview of the phylogenetic method

The basic premise underpinning the phylogenetic method is a simple one - once a sister group relationship between taxa has been demonstrated, their ranges in time can be equated to that of the oldest known representative. This premise is an extension of a general assumption of cladistic analysis – that speciation occurs by bifurcation, i.e. a taxon splits into two new daughter species, the morphology of the ancestral form will disappear and hence the ancestor will become extinct in the process (Hennig 1965; Doyle and Donoghue 1993). A logical rule of bifurcation is that sister taxa must have originated at the same point in time and so any given taxon must be as old as its sister (Fig. 2.1). The practical application of this rule, as embodied in the phylogenetic method, is to extend the stratigraphic range of many taxa backwards, regardless of their actual fossil occurrences.

The extension of a taxon's range back in time is known as a *ghost lineage*. A specific kind of ghost lineage that extends a group's (rather than a single taxon's) range back in time is known as a *ghost taxon*. A ghost taxon is simply the ghost lineage of a group that contains two or more taxa, and they correspond to the internal, or ancestral, segments of a cladogram. The time range added by ghost lineages and ghost taxa is known as the *ghost range*. The procedure for recovering ghost lineages within a clade from a combination of stratigraphic and cladistic data is outlined in Figure 2.2.

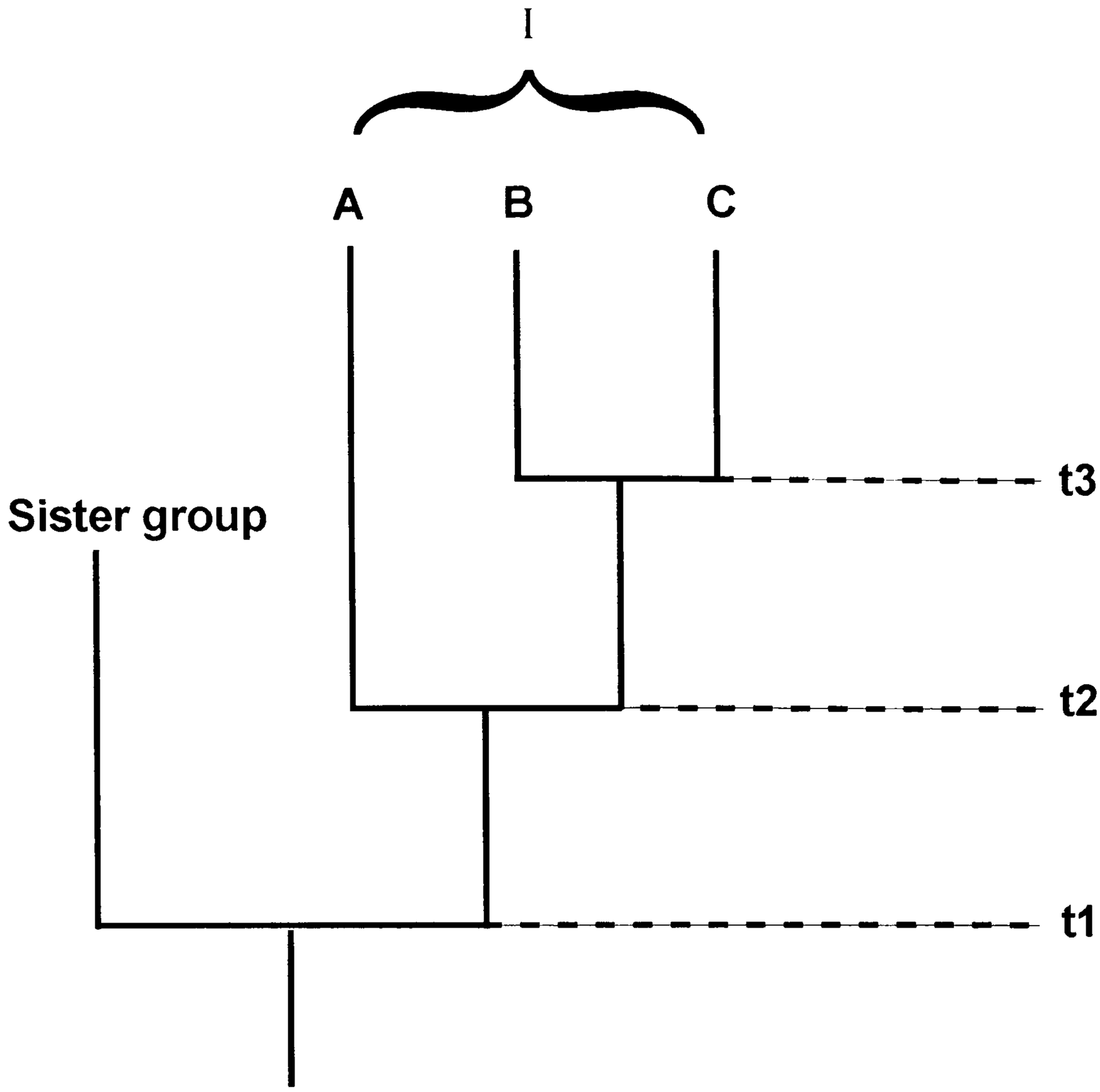


FIGURE 2.1. The implications of bifurcating speciation for origination times. This model of speciation dictates that sister groups must have the same time of origin. Group I consisting of crown taxa A, B, C plus stem lineages has a time of origin t1 which it shares with its sister group. Taxon A splits from the stem lineage of group B, C at time t2. Finally the two sister taxa B and C share an origination time of t3.

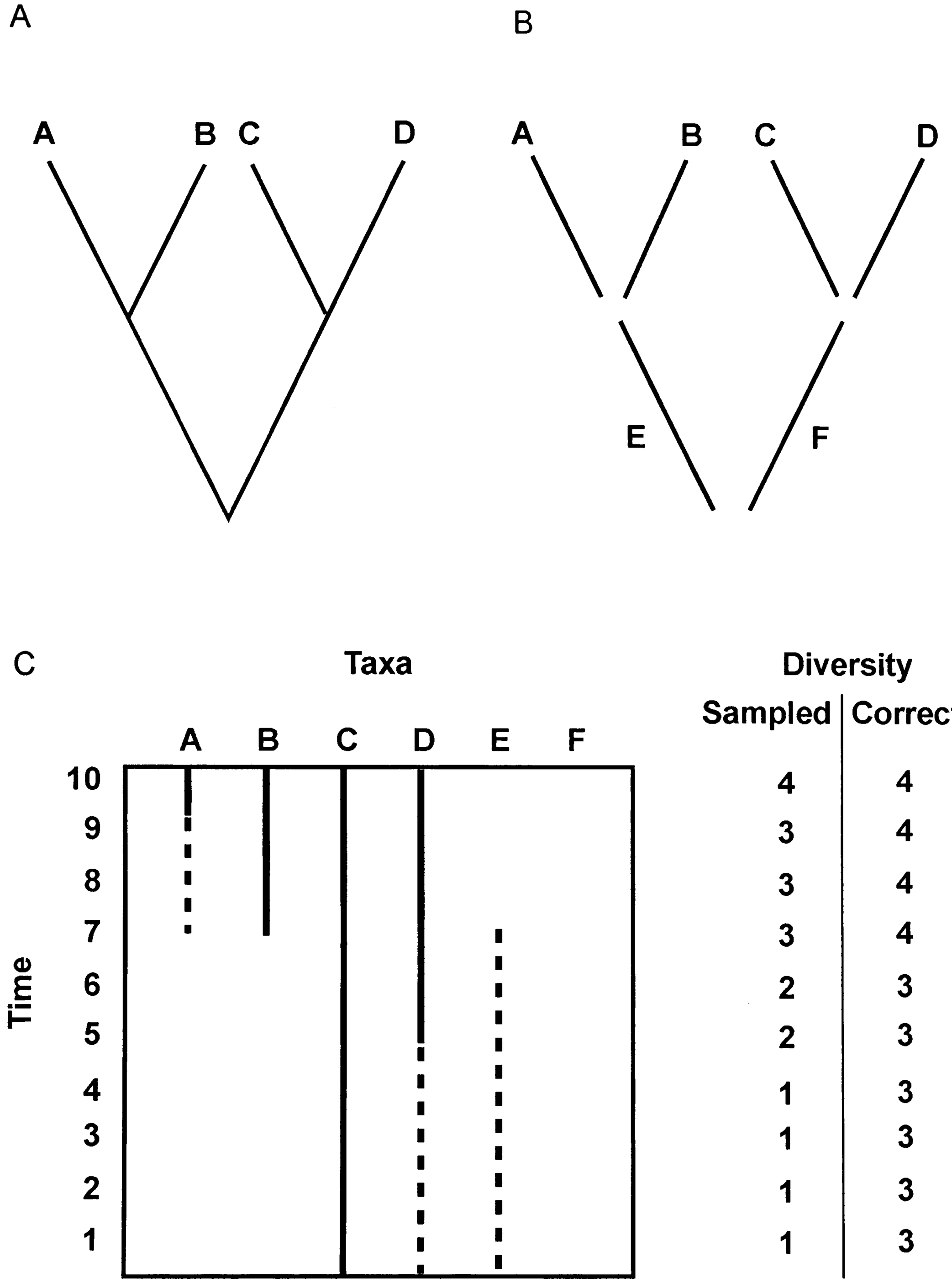


FIGURE 2.2. The methodology of the phylogenetic approach to diversity estimates. (A) A resolved phylogeny consisting of taxa A, B, C and D. (B) The phylogeny can be divided up into all of its component taxa, including taxa E and F which are ancestral to groups AB and CD respectively as predicted in the phylogeny. (C) Ghost lineages can be added according to the sampled ranges of the taxa. Taxon A has a ghost lineage extending its range down to time 7 where its sister taxon B originates. The same can be done for taxon D bringing its first appearance time to equal that of C. A ghost taxon E, equivalent to ancestral taxon E in the phylogeny, is created to extend the range of group AB down to that of CD. This diagram can be used to predict diversity, the figures to the right give the sampled diversity at each time interval as estimated by the taxic method, and the corrected diversity including ghost lineages (after Norell 1993).

The temporal extension of fossil ranges has huge consequences, not least for estimates of biodiversity through time. The phylogenetic method for estimating diversity sums not only the known fossil ranges occurring in any given time interval but also the ghost ranges added by cladistic interpretation. These ghost ranges produce an increase in diversity and often severely modify temporal diversity patterns (Norell 1993).

2.1.3. Problems with the phylogenetic method

There are several criticisms of the phylogenetic method of estimating diversity. Firstly it has been predicted that there is an inherent bias involved with only correcting the first appearance times of taxa and taxonomic groups (Foote 1996a; Wagner 2000). If a ghost lineage is the unsampled initial portion of a taxon's range, then the corresponding unsampled terminal portion can also be defined. The terms *artificial range truncation* (Signor & Lipps 1982), *Signor-Lipps* range (Wagner 2000) and *zombie lineage* (Sepkoski unpublished) have been suggested and the last is used here (Fig. 2.3), taken from the notion of a "zombie" representing the living dead. The extent of a taxon's zombie lineage can be inferred at some level of probability using the methods of Strauss and Sadler (1989) and Marshall (1990) but it cannot be inferred by phylogeny. If we assume that sampling at the end of a range is subject to the same biases as that of the beginning it must be assumed that the amount of zombie lineage in a sampled phylogeny will equal the amount of ghost lineage.

Wagner (2000) suggested that the ratio of ghost to zombie lineage depended upon sampling intensity, but he compared the amount of zombie lineage in a sampled clade against the amount of ghost lineage invoked by the combination of sampling and phylogeny, rather than the complete amount of ghost lineage present. The assumption of an equal ratio of ghost to zombie lineage in a sampled clade leads to the criticism that addition of ghost lineages results in a bias towards the early part as opposed to the end of time ranges, and hence a skew backwards in time in diversity counts. This criticism was investigated by Wagner (2000), by comparing diversity counts produced by the phylogenetic method as applied to the true tree and to the most parsimonious tree of a sampled clade. He did find an increase in diversity counts at the start of a clade's history using the phylogenetic method, but he did not specifically compare results from the phylogenetic method with the true diversity levels as obtained from the unsampled

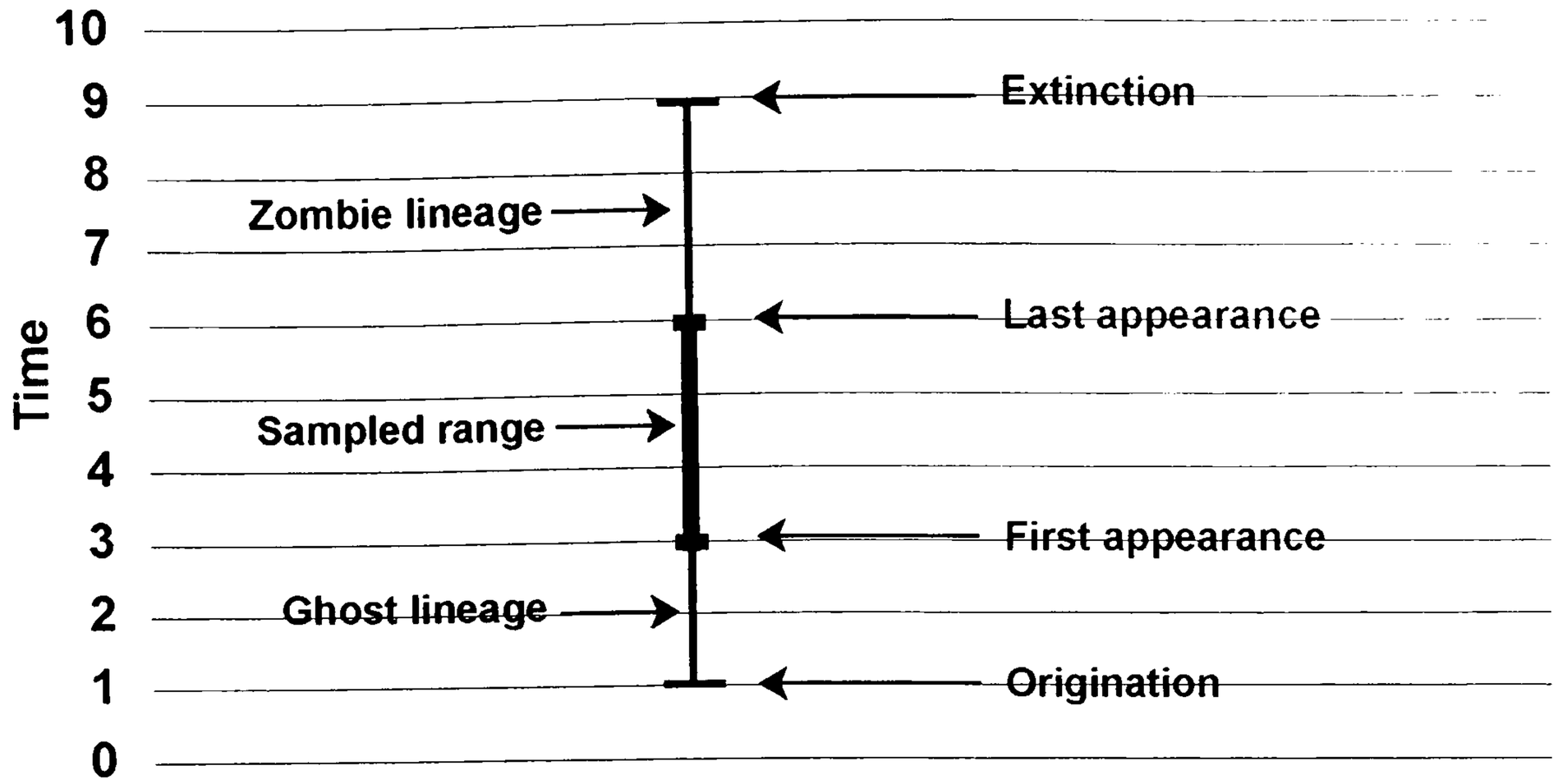


FIGURE 2.3. The terminology of taxon ranges. A taxon originates at time 1, but it is not sampled until time 3. This then becomes its first appearance in the fossil record. It is sampled finally at time 6 which becomes its last appearance. The sampled range of the taxon therefore runs from time 1 to time 6. The taxon's ghost lineage is that unsampled range before the first appearance, and its zombie lineage is the unsampled range after the last appearance. The phylogenetic method of estimating diversity is only able to recover some proportion of the ghost lineage. These terms can also be applied to the ranges of taxon groups as well as single taxa.

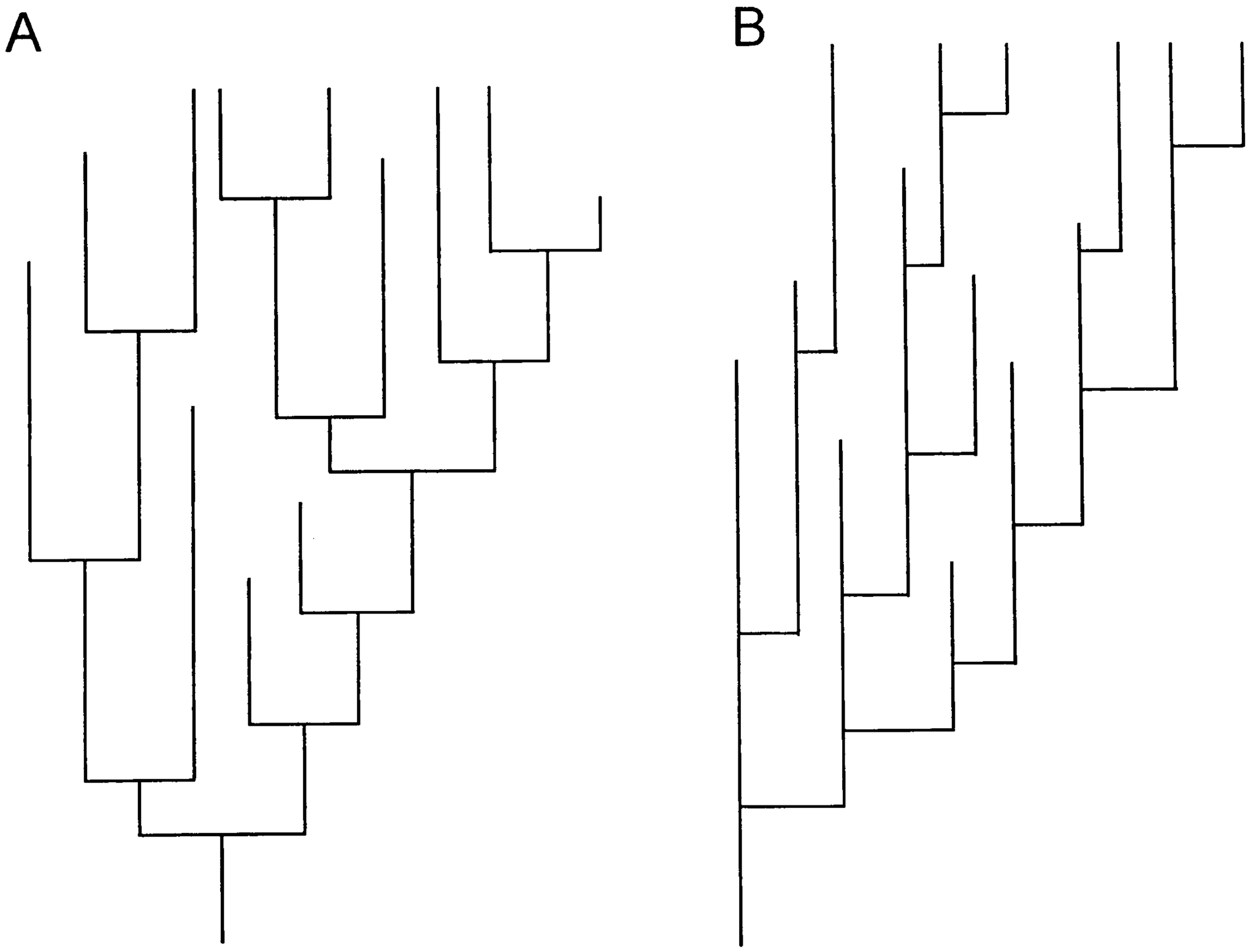


FIGURE 2.4. Bifurcating versus budding speciation models. (A) Speciation by bifurcation where the ancestral taxon gives rise to two descendent taxa simultaneously, becoming extinct at the same time. (B) Speciation by budding allows the concurrent existence of ancestral and descendent taxa, and the multiple origination of new species from one ancestor.

clade. Wagner's simulations created very small sampled clades (six species) that are not adequate for a robust assessment of the performance of the phylogenetic method.

Two further criticisms of the phylogenetic method stem from two assumptions often made when using cladistic analysis. The first is that speciation, or the origin of higher taxa, occurs by bifurcation and therefore two sister species arise at exactly the same point in time, corresponding to the point at which their ancestor goes extinct (Fig. 2.4A). This view of speciation is at odds with the multiple branching or "budding" speciation hypothesis (e.g. Mayr 1963; Eldredge and Gould 1972; and Fig. 2.4B) though it has received support (Vrba 1993). The bifurcation model is consistent with Hennig's (1965) rule that sister taxa must appear simultaneously and it is this assumption upon which the phylogenetic method is based (Norell 1993).

The second assumption often used in the phylogenetic method is that ancestral taxa are rarely found in the fossil record (Smith 1994). The creation of a ghost taxon to connect a sister group to its next nearest relative is in effect creating a ghost ancestor, a taxon represented by an internal segment of a cladogram (Norell 1993). However the cladistic method does not state that ancestors are never found, only that they are non-diagnosable, i.e. they can only be defined by a lack of characters. Thus many ancestral taxa may be included in cladistic analyses but defined as terminal taxa, especially if character loss is involved in bifurcation. Using empirically derived models of species origination, extinction and preservation, Foote (1996b) predicted that 1% - 10% of marine invertebrates in the fossil record are directly ancestral to other known fossil species. The logical outcome of the bifurcation model of speciation is that a third of fossil species should be ancestral, as every pair of sister species will have had an ancestor. The fact that the actual number is much lower may be due to co-incident preservation of ancestors and descendents, evidence for a budding rather than a bifurcating speciation pattern. Many population biology models imply that species properties encouraging speciation (e.g. wide geographic range and numerous populations within a species) also encourage preservation in the fossil record (Wagner and Erwin 1995). This is supported by molecular studies (e.g. Omland 1997) that show geographically widespread taxa tend to be paraphyletic compared to more restricted taxa. Hence there is evidence to suggest that taxa with many ancestral lineages also have an increased preservation potential. The unnecessary addition of ghost taxa in situations where sampled ancestors are misdiagnosed may seriously over-inflate estimates of diversity.

A final major drawback of the phylogenetic method is that it assumes that a 'true' cladogram for the group is available and that any errors in the inferred taxon relationships are minor when estimating diversity. In reality several well-supported cladograms are often available for any particular group, and the use of different trees results in very different reconstructions of biodiversity (Wagner 2000).

Although is has been claimed that the use of cladistic analysis to establish the sister group relationships among taxa, and infer unsampled range, is the best way to compensate for poor preservation in the fossil record (Smith 1994), there has not been a rigorous comparison between this method and other alternatives (Foote 1996a). In this chapter the performance of both the taxic and the phylogenetic methods of estimating diversity are tested, and two of the criticisms leveled at the phylogenetic approach are investigated: (1) that bias is introduced by correcting only the first appearance times of taxa, and (2) that error is introduced by including ancestral lineages in the analysis. The investigation is based on the use of a computer simulation of phylogeny growth and subsequent sampling.

2.2. Analysis methods

2.2.1. Use of computer simulations of phylogenetic systems

The unavoidable problem when trying to assess the usefulness of the various methods of enhancing diversity counts, such as adding ghost ranges, is that we have no idea how close we are to approaching the complete diversity count. One answer is to produce an artificial phylogeny using computer programs coded with algorithms to simulate the origination and extinction of taxa. An evolutionary tree can be 'grown' by such a program, its final topology dependent upon initial parameters input by the user, i.e. origination and extinction rates, and other options such as the simulation of mass extinction events and diversity equilibrium levels. The ultimate fate of a taxon is decided by random number generation, and so these models are known as *Monte Carlo* simulations. Such phylogeny modeling has become more prevalent with the increased use and power of personal computers, and has been instrumental in answering questions concerning the randomness of clade shape (Gould et al. 1977), and speciation (Bookstein 1987) and the effect of including paraphyletic taxa in diversity counts (Sepkoski & Kendrick 1993; Robeck et al. 2000) among others.

Sepkoski and Kendrick (1993) emphasized that Monte Carlo phylogeny generation methods have two distinct advantages:

1. Phylogenies can be studied with totally unambiguous ancestor – descendent relationships, something impossible in the real world.
2. Generation of phylogenies, fossil sampling and diversity estimation can be executed with explicit rules (i.e. computer algorithms) that can be subjected to focused criticisms and changed appropriately.

To this can be added the fact that the complete diversity history of a computer-generated phylogeny is known, against which any incomplete diversity counts whether taxic or enhanced, can be compared.

Unfortunately computer simulations are idealised and greatly simplified pictures of evolution, with many of the complexities of taxon origination and extinction either disregarded or averaged (e.g. origination and extinction rates), and based on a single theory of speciation, i.e. either multiple branching, or bifurcating speciation. However, they are useful in exploring end-member situations, for example exponential vs. logistic diversification, or mass extinction events vs. steady background extinction. More importantly they provide an experimental framework in which to test evolutionary hypotheses, and phylogenetic and diversity-summing methods.

2.2.2. The GHOSTRANGE program

2.2.2.1. Rationale and overview

A new computer program GHOSTRANGE was written in the C language for the IBM PC to investigate the impact of the addition of ghost lineages to estimates of diversity. This program is based on unpublished work by J. John Sepkoski Jr. and Christine M. Janis, and was written in collaboration with Dr. Janis. GHOSTRANGE is a Monte Carlo simulation of the growth of an evolutionary tree, starting from one taxon at time step 1, diversifying to a total of x taxa by time step n. The total number of taxa generated (x) is determined by the user. Thus both small (~100 taxa) and large (up to 1000 taxa) phylogenies can be generated. The program follows convention in using a time step interval of 1 million years, which should encompass the time necessary for speciation, local adaptation and biogeographic expansion (Sepkoski & Kendrick 1993).

Tree growth rate is controlled by origination and extinction rates input to the program, combined with random number generation. If an origination event occurs, it does so by bifurcation; i.e., one taxon splits to become two descendent taxa. These daughter taxa are distinct from each other, and are also distinct from the original ancestral taxon. Therefore the ancestor becomes extinct in the process of bifurcation (Fig. 2.5A). This mechanism of speciation is by no means universally accepted amongst evolutionary biologists (see Section 2.2.2.). Many speciation models, e.g. Mayr's peripatric model (see Mayr 1970), involve budding rather than bifurcating of species lineages. The multiple branching model has been used in previous computer simulations (e.g. Sepkoski and Kendrick 1993; Robeck et al. 2000; Wagner 2000). However, the bifurcation model is used here as Norell's (1992, 1993) method of estimating ghost lineages implicitly equates cladograms, with their bifurcating topology, to phylogenetic trees.

The phylogeny can grow either exponentially or logistically, and there is also an option to simulate mass extinction events. For a logistic pattern the origination rate is diversity-dependent, decreasing as the diversity level approaches the equilibrium level. Once this equilibrium is reached the origination rate is constantly adjusted as the diversity level changes, in order to maintain a steady-state.

Once a phylogeny is generated, it is then manipulated to test the two diversity-summing methods under investigation – the taxic taxon-counting method, and Norell's (1992, 1993) phylogenetic method of adding ghost lineages. Firstly the phylogeny is sampled uniformly according to a sampling rate input by the user. This gives each taxon a chance of being 'found' in any one time step, and simulates the sampling produced by preservation and discovery in the fossil record (Figs. 2.5B & C). A taxon is assumed to be present in all time steps between its first and last sampled appearance. Uniform sampling is extremely unlikely in the fossil record. However, earlier simulations using an irregular sampling algorithm revealed only trivial differences between the results of uniform and irregular sampling (Sepkoski unpublished), and so only the simpler, uniform sampling algorithm is used here. An option is also available to simulate "Pull of the Recent" (Raup 1979a), this assumes that all lineages surviving to the final time interval are extant and will always be found, i.e. a perfect sample. In reality the probability of all extant taxa in a clade being found in the Recent varies greatly from group to group, e.g. it is a reasonable assumption for mammal clades, but less so for invertebrate groups, and as such should only be interpreted as an end-member state.

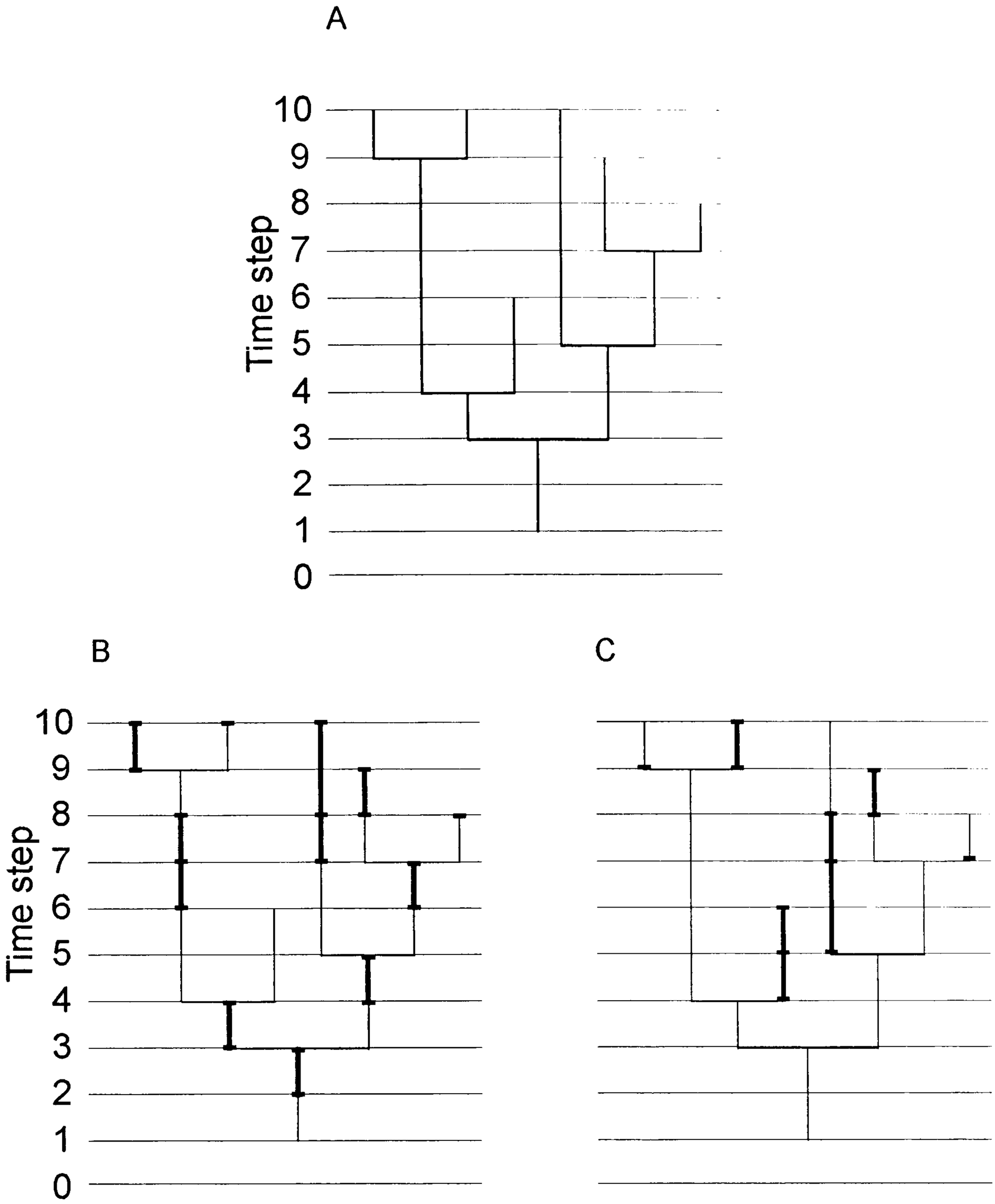
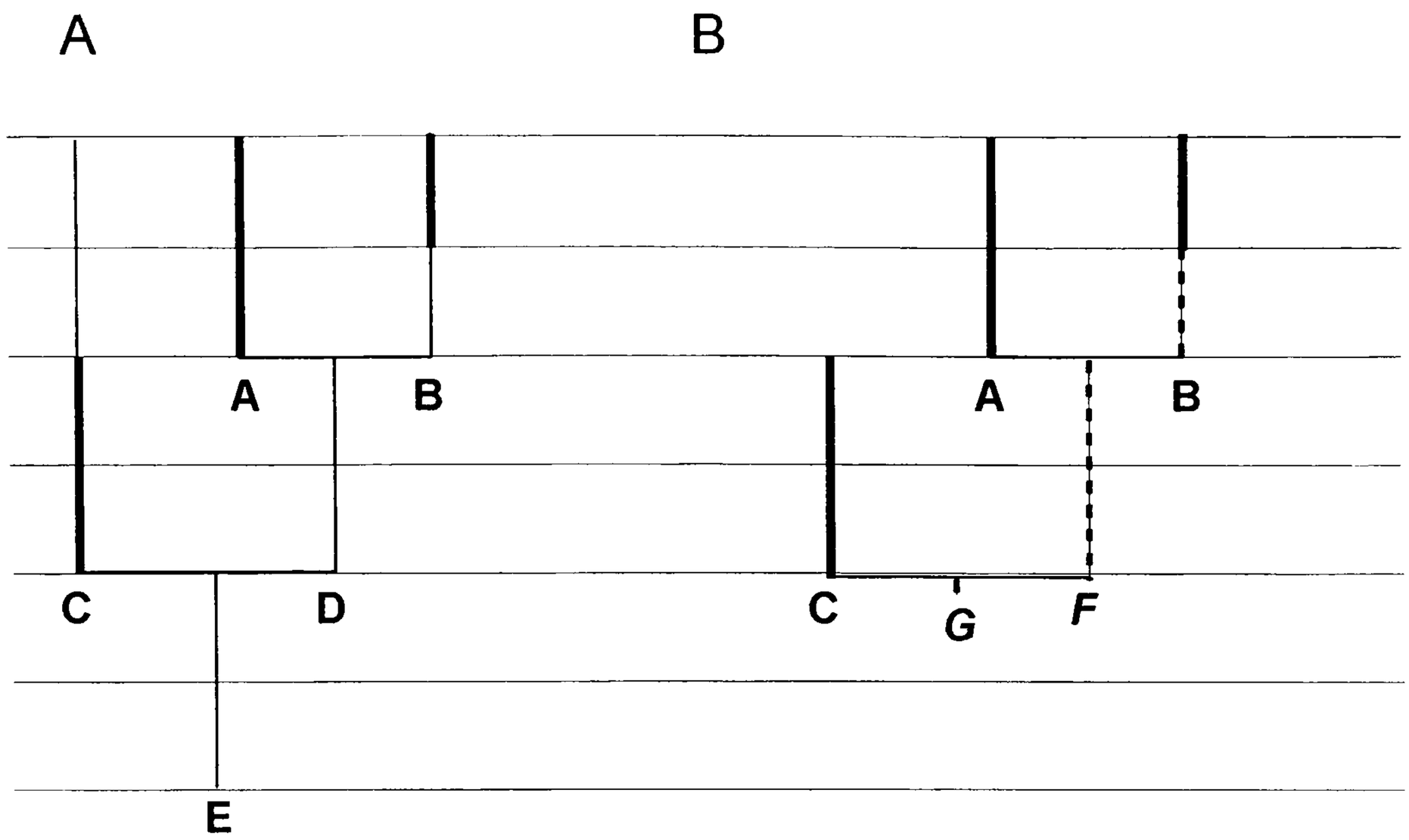


FIGURE 2.5. Creation and sampling of phylogenies using the GHOSTRANGE program. (A) A phylogeny is created starting with one taxon originating at time step 1. At each subsequent time step each taxon in existence has the opportunity to either bifurcate, to go extinct, or continue without bifurcation. The program ends once the desired number of taxa has been generated (in this case 11) and the final time step has played out. (B) The phylogeny is sampled. Each taxon is given the opportunity to be sampled during every time step that it has a presence in. A low sampling rate will produce singleton taxa. In this example the 'Pull of the Recent' option ensures all taxa extant in the final time step are sampled. (C) The same phylogeny is sampled, but this time ancestral taxa are excluded from the analysis. Only terminal taxa are made available for sampling.

Ghost lineages are now inserted into the sampled phylogeny. GHOSTRANGE reconstructs the relationships between the sampled taxa to form a new phylogeny based on the incomplete data. The gaps in the ranges and relationships of the sampled taxa are filled up with ghost lineages and ghost taxa according to Norell's (1992, 1993) methodology. The reconstruction of phylogenetic relationships is not based upon any cladistic analysis of character state distributions, as in Wagner's (2000) simulations. Such cladistic analyses merely provide a model of phylogeny. Rather, GHOSTRANGE reconstructs the relationships between taxa as derived from the perfectly known phylogeny created within the simulation. Hence the phylogenetic method is here being tested under the ideal situation of knowing the correct taxonomic relationships. In reality the performance of the phylogenetic estimate is effected by the robustness of the cladistic analysis, this is discussed in more detail in Section 2.4.

The procedure incorporates the assumption that ancestral taxa are rarely found in the fossil record, which is primarily made up of terminal taxa. Norell (1992) recognised that the assumption that ancestors are not represented was a weak one and he presented an adjustment to his diversity estimate method for situations where taxa ("parataxa") are suspected of being ancestors. Smith (1994) also suggested a method of inserting ghost lineages into phylogenies to account for ancestral taxa. The various ways of dealing with ancestral taxa are incorporated into the GHOSTRANGE program as follows. One option assumes that ancestors are never recovered from the fossil record: the program does not allow them to be sampled, (Fig. 2.5C) and they are not included in estimated diversity counts or ghost lineage insertion (Fig. 2.6). The second, perhaps more plausible option, allows ancestors to be sampled with as much likelihood as terminal taxa and to be included in the calculation of ghost lineages. Two versions of the GHOSTRANGE program were created with alternative algorithms to calculate the ghost lineages associated with ancestral taxa, These incorporate the two possibilities of ancestor diagnosis: (1) GHOSTRANGE_A: an ancestral taxon is mistaken as the sister taxon of its descendents, and therefore a ghost range is inserted from the first appearance of the descendent taxonomic group down to the *first* appearance of the ancestor (Fig. 2.7A). This mistake is a plausible one if bifurcations involve character loss making the ancestor potentially diagnosable, indeed the probability of this error increases as sampling intensity decreases since intermediate lineages between a sampled ancestor and its distant sampled descendents may not have been discovered. This mistake is simulated by inserting a ghost taxon between the first occurrence of a



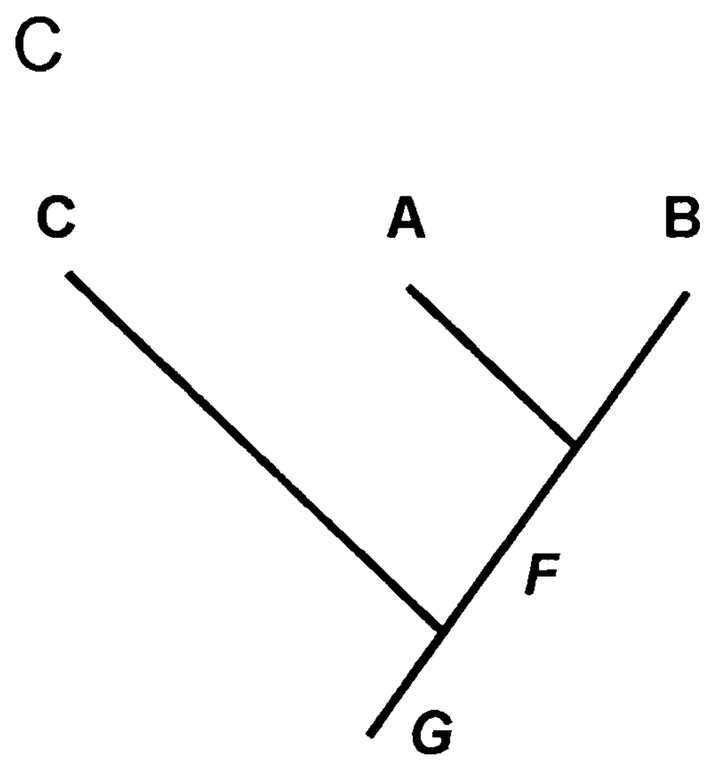


FIGURE 2.6. Ancestors not sampled. (A) A simple phylogeny is sampled (bold lines show sampled range), only terminal taxa are permitted to be found. (B) The GHOSTRANGE program adds ghost lineages (dashed lines) *sensu* Norell (1993). The first appearance of taxon B is extended down to equal that of A. A ghost taxon *F* is created to join group AB to its sister C. Finally a ghost taxon *G* is inserted to maintain the bifurcating nature of the phylogeny, but it is not included in diversity counts as it adds no range to the phylogeny. The phylogenetic method is able to recover the unsampled ghost lineage at the start of taxon ranges, e.g. taxon B, but not the unsampled zombie lineage at the end of taxon ranges, e.g. taxon C. (C) Phylogenetic diagram showing the correct relationships between the species with ghost taxa *F* and *G* occupying the internal ancestral segments.

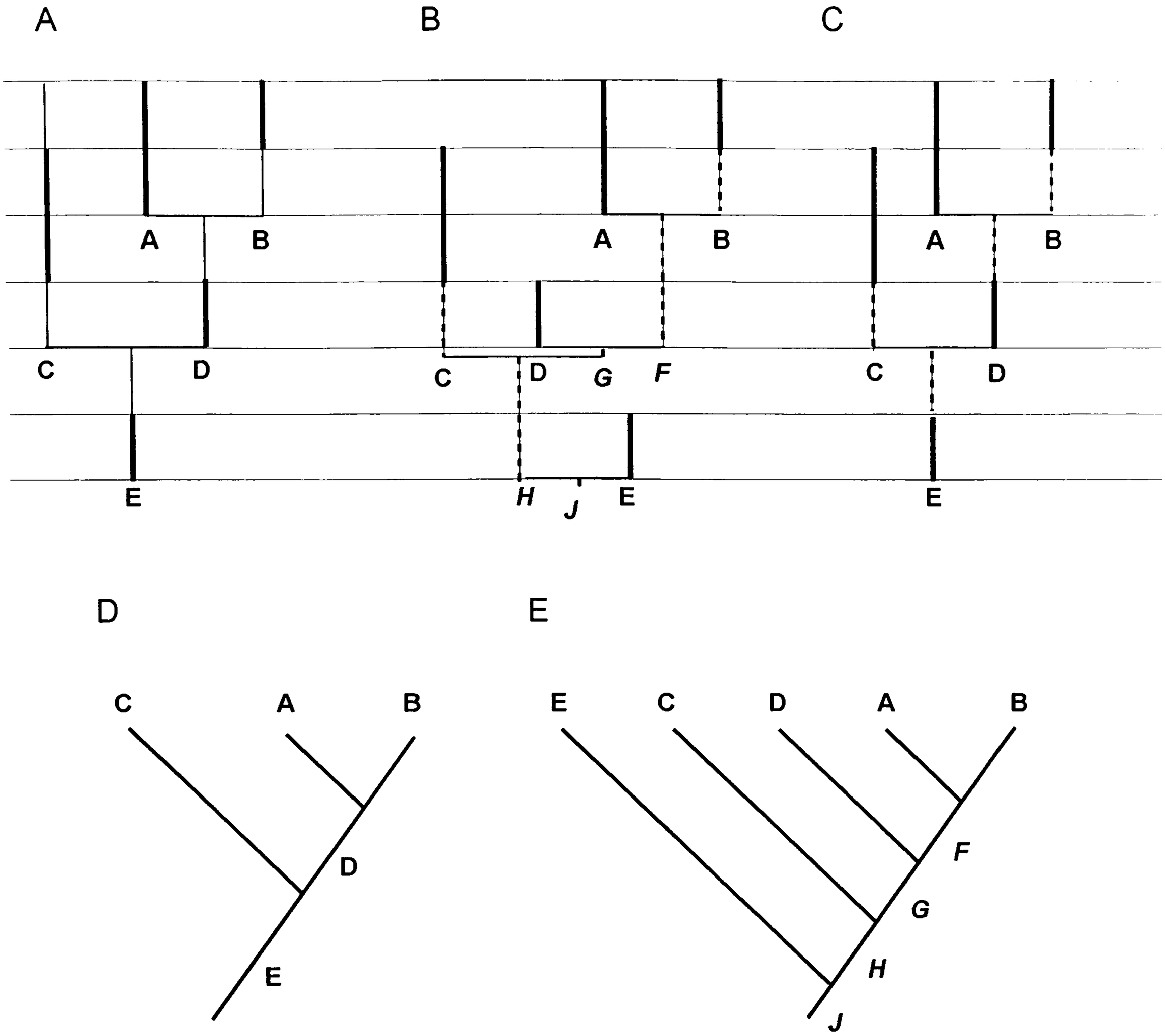


FIGURE 2.7. Ancestors sampled (A) A simple phylogeny is sampled (bold lines show sampled range). (B) In version GHOSTRANGE_A of the program ancestral taxa are treated as the sister taxa of their descendent groups (dashed lines show ghost lineages), for example taxon D is set as the sister of group AB, and a ghost taxon *F* is added accordingly. (C) In version GHOSTRANGE_B ancestral taxa are correctly identified, and the ghost lineage of a descendent group are only extended to the last appearance of their ancestor (cf Smith 1994). Hence a ghost lineage is extended from the first appearance of group AB to the last appearance of taxon D. Using this method the phylogenetic estimate is able to recover the zombie lineages of ancestors, e.g. taxon D, but not those of terminal taxa, e.g. taxon C. (D) Phylogenetic diagram showing the correct relationships between the taxa. (E) The form of the diagram if ancestors are misdiagnosed as the sister taxa of their descendent groups. Using these relationships the GHOSTRANGE_A program inserts ghost lineages as shown in B. The newly created ghost taxa *F-J* fill in the internal segments of the cladogram.

sampled sister group and the first appearance of its most recent sampled ancestor. (2) GHOSTRANGE_B: Ancestral taxa are correctly diagnosed, and ghost lineages are therefore inserted from the first appearance of a descendent group only to the *last* appearance of the sampled ancestor (Fig. 2.7B). Using this method the phylogenetic estimate is able to recover the zombie as well as the ghost lineages of ancestral taxa. However, the manner of dealing with ancestors does not alter the inability of the phylogenetic method to recover the zombie lineages of terminal taxa.

Following insertion of ghost lineages and taxa, three diversity counts are produced. The first is the actual taxon count per time step compiled from the original unsampled phylogeny. The remaining two are the diversity estimates based on the two methods under test. The uncorrected diversity estimate is the taxic method, simply summing the number of sampled taxa in each time step. The corrected diversity count not only sums all sampled ranges but also all ghost lineages with a presence in each time step. The two diversity estimates are compared with the complete data to assess how well each has performed in capturing both the magnitude (percentage of) and the pattern of the real diversity count. Pattern comparisons are made using the squared product-moment correlation coefficient (R^2) and also the squared partial correlation on time removed (see Section 2.2.2.3).

2.2.2.2. Parameters and options

See Appendix I for GHOSTRANGE_A and _B program source code and Appendix IIb for user instructions. The programs are contained on the IBM disc accompanying this thesis.

The following parameters and program options must be entered for each run:

- Number of taxa. This is the total number of taxa to be generated in the program run. Once this number is reached the program will allow the current time step to be completed, i.e. all further extant taxa will have a final opportunity to bifurcate or go extinct. Therefore the final number of taxa generated is likely to be slightly above the figure input by the user.
- Initial origination rate 0-1.
- Initial extinction rate 0-1.

- Equilibrium level. This is the diversity level around which the user wants diversity to fluctuate in a logistic diversification pattern. If an exponential pattern is required, zero is entered, and origination and extinction rates remain constant throughout the program run (barring mass extinction events – see below).
- Mass extinctions included. If this option is selected, at regular intervals in the life time of phylogeny growth the background extinction rate is raised to simulate a mass extinction event.

If a phylogeny goes extinct before reaching the required number of taxa, an error message is displayed and the program must be re-run. Once a complete phylogeny has been successfully generated it can then be submitted to sampling and ghost range insertion, with the following parameters and options:

- Sampling rate 0-1.
- "Pull of the Recent" included. This option sets the sampling rate for the final time step to 1. Hence the point-count of sampled taxa at the end of the program run will be equal to the total number of taxa still extant.
- Ancestors included. This is the option that determines how ancestral taxa are to be treated in the analysis. Including ancestors will allow ancestral taxa to be sampled and incorporated in the insertion of ghost ranges. How the ghost ranges are inserted depends upon which version of the program is in use (see Section 2.2.2.3 below).
- Singletons included in diversity counts. A taxon is normally counted as present within a time step if its sampled range runs right through the step. Singleton taxa, those that are only sampled once, cause a particular problem in diversity counts, as a decision must be made about which time step to include them in. The user has the option of avoiding these problems by choosing not to include singleton taxa at all in diversity counts.

Once these parameters have been entered, the program will run and output the resulting diversity counts and correlation coefficients as a Microsoft Excel spreadsheet file, name chosen by the user. There is then the option of performing another analysis on the same phylogeny using different sampling and ancestor options. The user may

perform any number of analyses on one phylogeny, thus increasing the comparability of results.

2.2.2.3. Algorithms

Creating phylogeny

A phylogeny starts off at time step zero with no taxa. At time step 1, taxon 1 originates. At time step 2, taxon 1 has the opportunity either to split into two descendent taxa, at which point it becomes extinct, to go extinct without splitting, or to do nothing. The behaviour of taxon 1 and each subsequently extant taxon within each time step is determined by random number generation. The random number generator used by the GHOSTRANGE program is one of the RanRot families of pseudo-random number generators, developed by Agner Fog (http://www.agner.org). A random number in the range 0-1 is compared with the origination and extinction rates to determine what the fate of the taxon will be. If the random number is smaller than the rate, the corresponding event will occur. Therefore the higher the rate, the more likely the event. If an exponential diversity pattern is required, origination and extinction rates remain the same throughout the program run. For a logistic pattern the origination rate is diversity dependent, decreasing as diversity approaches the equilibrium level. Once this level is reached the origination rate is constantly adjusted as the diversity level changes, in order to keep diversity fluctuating around the equilibrium level. The equation for calculating the diversity-dependent origination rate is:

$$r_s = k_s - D\left(\left(k_s - r_e\right) / D_{eq}\right) \qquad \text{(eq. 2.1)}$$

where:

r_s = diversity-dependent rate of origination

k_s = initial rate of origination

r_e = rate of extinction

D = standing diversity

D_{eq} = equilibrium diversity.

This equation is derived from a combination of Sepkoski's (1978) models for diversity dependent per-taxon origination and extinction rates (Chapter 1, Equation 1.13, 1.14) , and the equilibrium diversity constant (Chapter 1, Equation 1.15)

In this case the slope of the per-taxon extinction rate function (*b* in equation 1.14) equals zero, as the program uses a constant extinction rate except during mass extinction events.

Mass extinctions are simulated by GHOSTRANGE using the procedures of Sepkoski and Kendrick (1993) and Robeck et al. (2000). At intervals through the program run (arbitrarily set to every 20 time steps) the background extinction rate is increased to 0.9 for one time step only. Extinction rate is then returned to its original level, and diversity bounces back exponentially, or logistically to equilibrium, depending on the diversification model in use.

As each taxon is created it is given a unique ID number, a *real* first appearance time and a generation number, with taxon 1 having generation number 1. When each taxon goes extinct it is given a *real* last appearance time. If a taxon persists to the end of the time line, it is given a real last appearance time equal to the succeeding time step indicating it remains extant at the end of the run.

Each taxon is linked to its ancestor and to its two descendents (if it has any). This is known as a *linked binary tree* in the C language and mimics the bifurcating nature of the phylogeny. In addition each taxon is linked to its sister taxon, i.e. if taxon 1 gives rise to two descendents, taxa 2 and 3, these two descendents will be linked to each other. This facilitates the addition of ghost lineages and taxa after the phylogeny has been sampled. The final time step of the program run occurs once the required number of taxa have been generated. All taxa extant in the final time step are cycled through the origination and extinction algorithms before phylogeny growth ceases, hence the final tree size will be slightly larger than that requested by the user.

Sampling phylogeny

Every extant taxon may be sampled in each time step. Exceptions to this are ancestral taxa, which are excluded from the sampling algorithm if the option to include ancestors is not taken. Whether a sampling event occurs or not is determined by comparison of a random number with the sampling rate input by the user. The first time step in which a taxon is sampled is set as the *uncorrected* first appearance of that taxon. The last time step in which a taxon is sampled is set as the *uncorrected* last appearance of that taxon. This simulates the sampling of a phylogeny produced by an incomplete fossil record.

Reconstructing phylogeny and inserting ghost ranges

The program seeks the nearest sampled relative of each sampled taxon. It searches through the phylogeny in the order: taxon's descendents, sister, sister's descendents, ancestor, ancestor's sister and descendents, next ancestor, and so on, until a sampled relative is found. Once such a sampled relative is identified, unless it is closer to another sampled taxon, it is identified as the new sister to the original taxon. Thus if the phylogenetic option of the program run is set to include ancestors, there is the chance that a taxon will be identified as sister of one of its own descendents.

If the GHOSTRANGE_A version of the program is in use, the first appearances of the new sister taxa are then simply equalised, potentially adding a ghost lineage to the range of one of the taxa. These are known as the *corrected* first appearances. As soon as a sister pair is matched in this way, a new ghost taxon is inserted into the phylogeny as ancestral to the two. This ghost connects the group to their next nearest relative, which can then be found. If the next nearest relative has a sampled first appearance earlier than that of the sister pair, the range of the ghost taxon will be extended down to this point. If however the next nearest relative has a sampled first appearance later than that of the sister pair, the range of the relative will be extended, not that of the ghost taxon. This leaves a ghost taxon with a range of 1 time step, a singleton. Such singleton ghost taxa are not included in the corrected diversity counts. Although they are theoretically required in the reconstructed phylogeny, to maintain the bifurcating principle of origination, they do not add any range to the phylogeny, and are not included in Norell's (1992, 1993) theory of inserting ghost ranges. Once a ghost taxon has been inserted into the corrected phylogeny, it is treated like any other taxon, i.e. a ghost taxon will end up as a matched sister to a 'real' taxon or to another ghost taxon, and it may have its range extended accordingly. This process of adding ghost lineages and ghost taxa continues until all taxa are re-matched with a sister species, and the new phylogeny reconstructed. At this point groups are no longer separated by any time range gaps.

The alternative version of the program, GHOSTRANGE_B, uses an algorithm for calculating ghost lineages that incorporates Smith's (1994) correction for taxa suspected of being ancestors. Here, if the nearest sampled relative of a taxon is identified as ancestral to the taxon, the first appearances of the matched 'sisters' are not equalised, instead the first appearance of the descendent is only extended down to the *last* appearance of the ancestor. This is the *corrected* first appearance of the descendent, the first appearance of the ancestor remains the same. An ancestral ghost taxon for the

pair is then inserted in the same way as described above, and the program moves on to the search for the next nearest relative. Once again, if the next nearest relative is identified as ancestral to the original pair, the corrected first appearance of the new ghost taxon is set to equal the *last* appearance of the ancestor. Using this version of the program, the phylogenetic method was tested under conditions simulating the correct diagnosis of ancestors within a phylogeny. Within the simulation the ancestral taxa are known, however in reality the ancestral status of any taxon would have to be inferred.

Summing diversity

The diversity count for any given time step is the sum of those taxa that range from the start of the time step to the start of the next time step, e.g. diversity at time step 2 includes those taxa that range from step 2 to step 3 (Fig 2.8A). Three counts are made, for the actual ranges of the taxa, the uncorrected ranges (i.e. the taxic estimate) and the corrected ranges (i.e. the phylogenetic estimate). Diversity counts for the final time step include all extant taxa. Singleton taxa, those sampled in only a single time step, are a problem when summing the uncorrected and corrected diversity counts. The question of which time step to count them in has been resolved somewhat arbitrarily by examination of their actual range through time (Fig. 2.8C). This ensures that no singleton taxon is counted in a time step where their actual range would not be counted. This problem is avoided if the program option to exclude singleton taxa is selected.

Comparing diversity counts

The two estimated diversity patterns are compared with the real pattern using two statistical metrics, the squared product-moment correlation coefficient (R^2) (Fig. 2.9A), and the squared partial correlation coefficient with correlation on time removed (Fig. 2.9B). The simple R^2 value can give misleading results when applied to time series data such as diversity counts (see Connor 1986; Harvey and Pagel 1991) and so the second metric is used on time de-trended data. This statistic is essentially the R^2 value between residuals calculated from linear regressions of the data on time, and it tests whether the deviations from expected diversity for one curve predict the deviations from expected diversity for another. Hence the partial R^2 value gives an indication of how good the match is between the real and estimated diversity patterns, in terms of the correlation between the magnitudes of diversity increases and decreases as displayed by the two

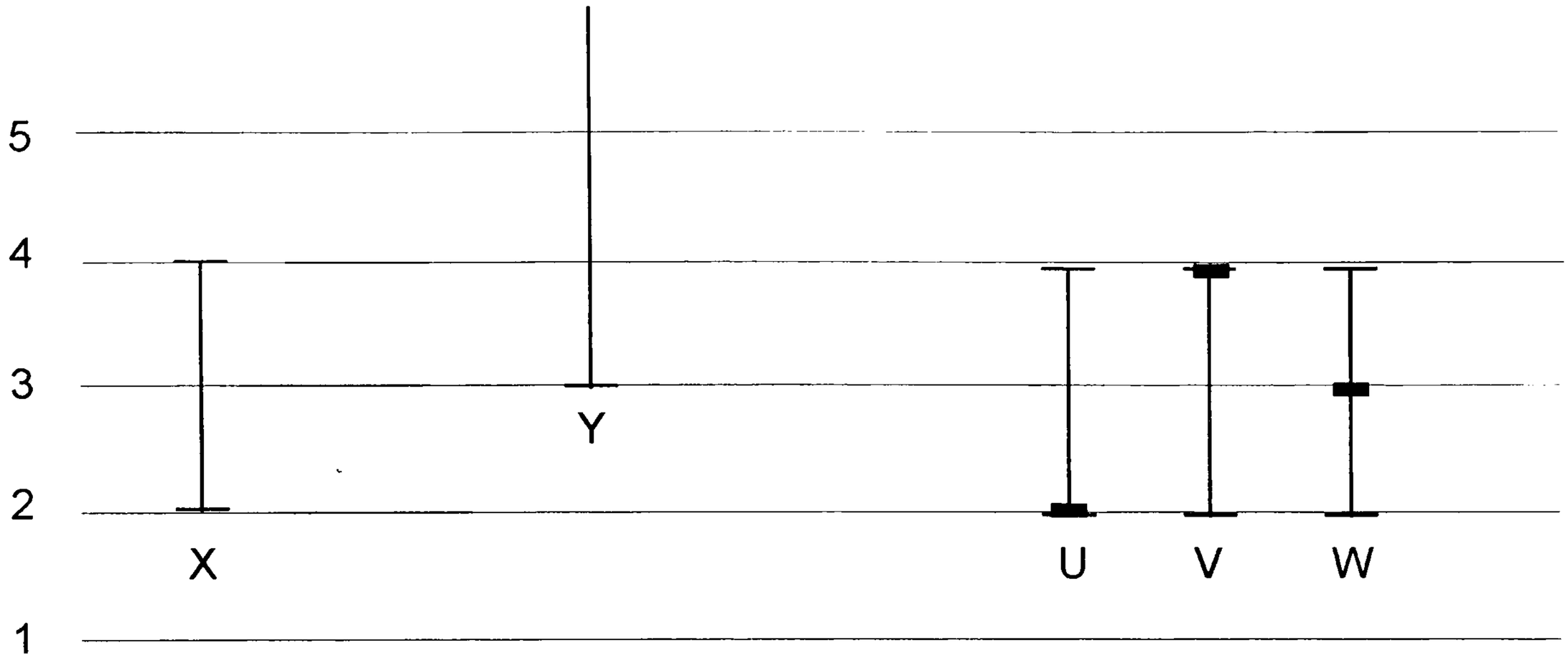


FIGURE 2.8. Summing diversity. (A) Diversity is summed by GHOSTRANGE at each time step, and includes all taxa with ranges running from the start of the time step through to the start of the next time step, e.g. taxon X will be included in the diversity count for time step 2 and time step 3, but not that of time step 4. (B) GHOSTRANGE takes a point count of all taxa extant at the end of the time period, step 5, e.g. taxon Y. The final range-through count is taken for the penultimate time step, in this case step 4. These two counts will be the same for the real diversity count, but may be different for the sampled count due to singleton taxa. (C) When calculating sampled diversity GHOSTRANGE includes singleton taxa in the time step that the actual range of the taxon runs through, e.g. taxon U is sampled (bold line) at time step 2 and counted in time step 2. Taxon V is sampled at step 4 but counted in step 3. If the taxon has a range on both sides of the sampling point (e.g. taxon W) it is counted in the step above. Although somewhat arbitrary, this method of counting singletons ensures that no taxon's sampled range can be counted outside of its actual range, and also ensures that no ancestor is counted in the same time step as its descendants.

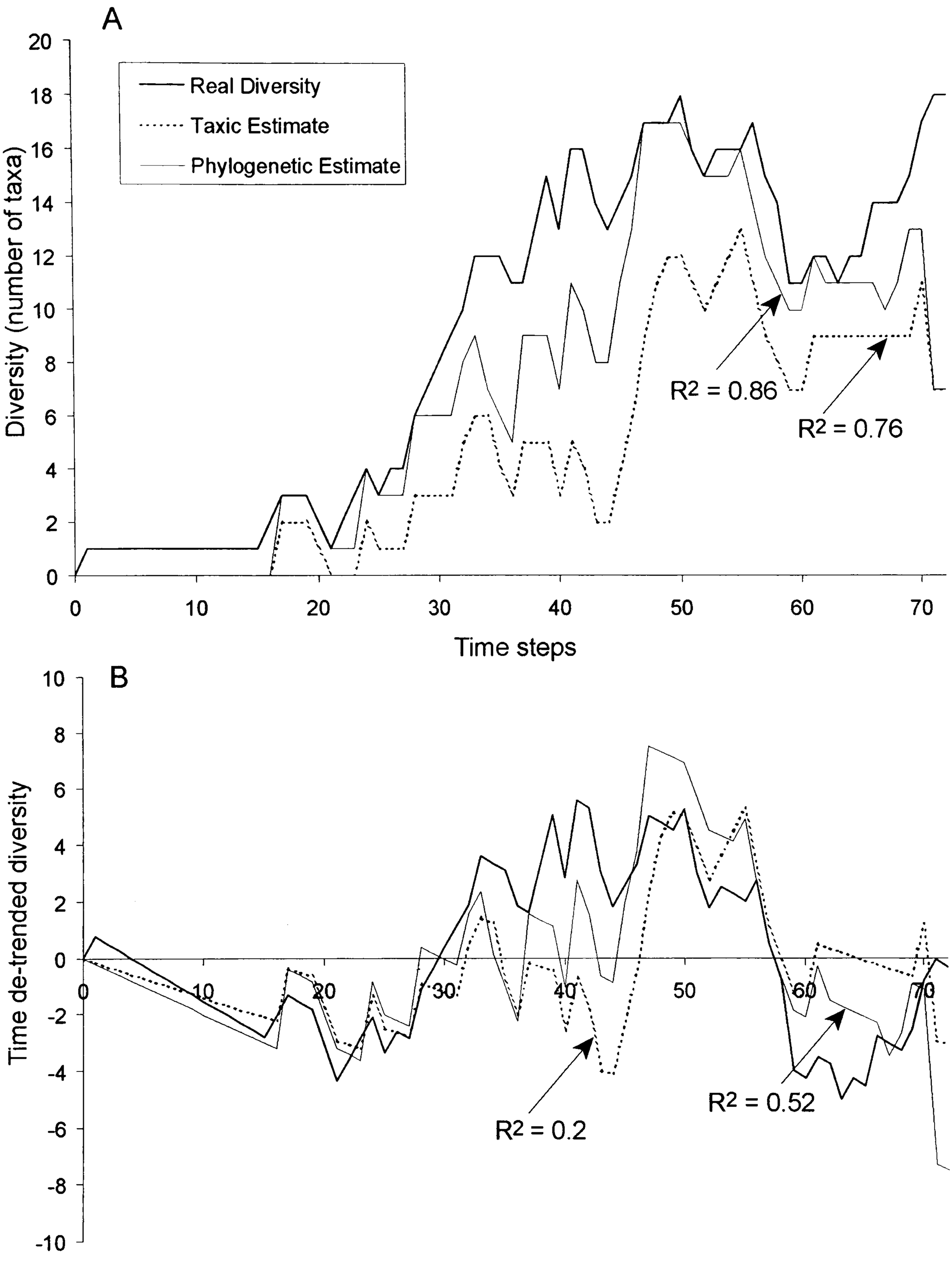


FIGURE 2.9. Assessing the performance of diversity estimates (A) Each estimated diversity pattern is compared to the real pattern using the squared product moment correlation coefficient (R^2). (B) A more accurate comparison is obtained by using the squared partial correlation coefficient on time removed. All three data sets are de-trended by plotting the residuals of linear regressions on time. This calculates the match between data sets independent of any linear increase or decrease in diversity, it generally gives lower R^2 values due to this removal of time trends.

curves. As such has been used in previous computer simulations of diversity curves (Sepkoski & Kendrick 1993; Robeck et al. 2000).

Results output

Each single analysis generates a file output detailing all parameters and options chosen for that run, statistical results, plus the complete diversity listing for each time step. This listing comprises real, uncorrected, and corrected diversity counts; time de-trended uncorrected/corrected diversity counts; and uncorrected/corrected diversity magnitude. In addition, to facilitate comparability, each phylogeny is complemented by a master-file output containing a summary of options and parameters, and statistical results for every analysis that is carried out on that phylogeny.

2.2.3. Parameters used

The initial analysis was performed using only the GHOSTRANGE_A version of the program, to investigate the effect of misdiagnosis of ancestral taxa. The aim was to provide results for as wide a range of parameter values as possible. Sixteen phylogenies were produced using the following generating parameters:

- Number of taxa. For 'small' phylogeny generation a figure of 100 was input, and for 'large' phylogenies this was increased to 500. The final size of each phylogeny was always slightly over these values (see Section 2.2.2.3.). This covers the range from average size cladistic studies to very large investigations.
- Initial origination rates were set at either 0.25 and 0.35, extinction rates at 0.05. These rates are reasonable for fossil genera in radiating clades. Rates for fossil genera are more appropriate than for species as few large cladistic studies are carried out at species level.

These values were used to generate phylogenies using both exponential and logistic growth patterns and both including and excluding mass extinctions. Each phylogeny was then sampled multiple times using sampling rates of either 0.1 or 0.5. A probability of 0.5 occurrences per million years is very high for most fossil taxa, but a high sampling rate was included to investigate subtle differences between the two estimates of diversity. A rate of 0.1 occurrences per million years is plausible for genera within a

well-preserved clade. All combinations of program options (ancestors included, 'Pull of the Recent' imposed, singletons counted) were run for each sampling rate. This gave a total of 16 analyses for each of the 16 phylogenies – a total of 256 runs for this initial investigation.

The results of this first stage were analysed and further program runs performed to investigate parameters and diversification scenarios identified as significant to the performance of the phylogenetic estimate (Section 2.3.2). The GHOSTRANGE_B version of the program was then used to test the performance of the phylogenetic estimate assuming that ancestral taxa are correctly diagnosed (Section 2.3.3).

2.3. Results

A series of Excel files containing the summarised results of all GHOSTRANGE analyses performed for this research may be found on the IBM disc accompanying this thesis. A description of the files is contained in Appendix IIa.

2.3.1. GHOSTRANGE_A initial analysis

The results of the initial analysis investigating the effect of all combinations of parameters in small and large clades are shown in Table 2.1. The GHOSTRANGE_A version of the program was used, hence if ancestors were sampled in the analysis they were misdiagnosed as the sister taxa of their descendents.

	Parameter value	Taxic diversity		Phylogenetic diversity	
		Mean partial R^2	Mean maximum diversity magnitude (%)	Mean partial R^2	Mean maximum diversity magnitude (%)
Small clades	Exponential	**0.59**	76	**0.61**	**121**
	Logistic	0.36	85	0.66	**135**
	MEx not included	0.47	82	0.63	**131**
	MEx included	0.47	80	0.63	**125**
	SI = 0.1	0.28	72	0.51	**112**
	SI = 0.5	0.66	90	0.76	**143**
	PR not included	**0.5**	62	**0.54**	**123**
	PR included	0.45	100	0.73	**133**
	Ancestors not sampled	0.42	72	0.65	89
	Ancestors sampled	0.52	89	0.62	**166**
	Singletons not included	0.42	78	0.63	**124**
	Singletons included	0.52	84	0.64	**132**
Large clades	Exponential	**0.66**	77	**0.66**	**112**
	Logistic	0.53	81	0.81	**127**
	MEx not included	0.62	80	0.77	**120**
	MEx included	0.56	77	0.7	**119**
	SI = 0.1	0.38	69	0.63	98
	SI = 0.5	**0.8**	89	**0.83**	**141**
	PR not included	**0.67**	57	**0.63**	**115**
	PR included	0.52	100	0.83	**124**
	Ancestors not sampled	0.55	70	0.78	85
	Ancestors sampled	**0.64**	88	**0.69**	**155**
	Singletons not included	0.56	76	0.74	**113**
	Singletons included	0.62	82	0.73	**125**

Table 2.1. Summary of results from initial 256 runs of GHOSTRANGE_A program. Data shown are mean values for all runs incorporating the stated parameter on either small or large phylogenies, *n* in each case is 64. Mean partial R^2 values are shown in bold where the uncorrected diversity R^2 is less than or almost equal to (within + 0.05) the corrected diversity R^2. Mean maximum diversity magnitudes are shown in bold where they exceed 100%. Mex = mass extinctions, SI = sampling intensity, PR = 'Pull of the Recent'.

Strength and significance of the correlations

The mean partial R^2 values in Table 2.1 show the *strengths* of the correlations between the real data and the estimates. For example a small clade with an exponential diversification pattern has an average uncorrected partial R^2 of 0.59 – 59% of real pattern is being captured by the uncorrected estimate, a correlation of medium strength. In contrast large clades with a logistic diversification pattern have on average 81% of real pattern captured by the corrected estimate, a fairly strong correlation. However the *strength* of correlation should not be confused with its *significance*. Significance is a statistical concept that can be calculated readily knowing both the R^2 value of a correlation and the sample size (i.e. number of time steps). The lower that each of these values becomes, the less significance can be attached to the correlation. Therefore significance gives a measure of the probability that a correlation could have occurred by chance, regardless of its strength.

All 256 runs in the initial analysis were tested for the significance of their uncorrected and corrected data correlations (partial R^2 values) using a *t*-test. The results show that in 215 (84%) of the runs both the uncorrected and corrected estimate correlations are statistically significant at the 0.05 level. This demonstrates that these experimental results can be relied upon as a genuine statistical test of the performance of the two diversity-summing methods under investigation. The cases where the correlations are not significant at the 0.05 probability level are those where the sample size is low (i.e. a relatively small number of time steps) and the correlations are very weak. In a small number of cases an R^2 value of 0 was discovered for a correlation; this indicates that there was no match between the real data and the diversity estimate. For correlations approaching this level of weakness it is very difficult to prove statistical significance without running a very large number of time steps. For example to demonstrate the statistical significance of a weak correlation $R^2 = 0.008$ a 500 step run would be required. Therefore in the following results very weak correlations ($R^2 < 0.1$) may not be statistically significant if there are a small number of time steps. However, increasing the number of time steps of these runs would only increase the *significance* of the weak correlation, it would not *strengthen* the correlation.

In the majority of the initial 256 program runs, the corrected diversity estimate captures the pattern of real diversity much better than the uncorrected estimate. The mean partial R^2 values for the corrected count are significantly (> +0.05) better than those of the traditional count in 171 out of the 256 simulations (67 %). Examples are

shown in Figure 2.10. There are two exceptions to this general rule: where the taxic count is on a par with, or (as in 23% of program runs), exceeds the phylogenetic estimate. Firstly the performance of the taxic method equals that of the phylogenetic method with an exponential diversification pattern, in contrast to logistic patterns where the latter invariably (though not always) out-performs the former. While switching to an exponential from a logistic pattern increases the reliability of the taxic method, it decreases that of the phylogenetic estimate. The same is true for inclusion of the 'Pull of the Recent'. If all taxa are permitted to be sampled in the final time interval of the program run, the corrected count performs better than the uncorrected. However if Pull of the Recent is not simulated the performance of the corrected count significantly drops, while the opposite is true of the taxic method which equals, or out-performs it. These scenarios are investigated in more depth below (Section 2.3.2).

The corrected diversity estimate, which includes ghost ranges, significantly over-estimates diversity magnitudes in the many of program runs. In 100 of the simulations (39%) the mean maximum diversity of the corrected estimate exceeds that of the real data. These are situations where ancestors are sampled and misdiagnosed as sister taxa of their descendents. Stripping of ancestors may eliminate as many as 50% of a phylogeny's taxa, severely reducing the magnitude of diversity captured by the taxic method. When ancestors are included in the analysis, further inclusion of ghost taxa increases the diversity magnitude estimates of the phylogenetic method by anything up to double the actual count. Inclusion of ancestors actually reduces the mean partial R^2 value for the phylogenetic method from 0.65 to 0.62 for small clades, and from 0.78 to 0.69 for large clades. In contrast ancestor inclusion causes the taxic method to perform better, increasing from 0.42 to 0.52 for small clades and from 0.55 to 0.64 for large.

The inclusion of mass extinctions in phylogeny generation does not greatly effect the amount of *pattern* capture achieved by the two estimates, though earlier simulations suggest that diversity *magnitude* capture is affected (Sepkoski unpublished). This hypothesis, and the effect of the inclusion of ancestors, are tested in further simulations (Section 2.3.2).

The exclusion of singleton taxa from diversity counts does not greatly affect the estimates, particularly using the phylogenetic method. This is probably because the ranges of singleton taxa present in a sampled phylogeny, which are excluded from the uncorrected diversity count, are often extended by ghost lineages, and therefore no

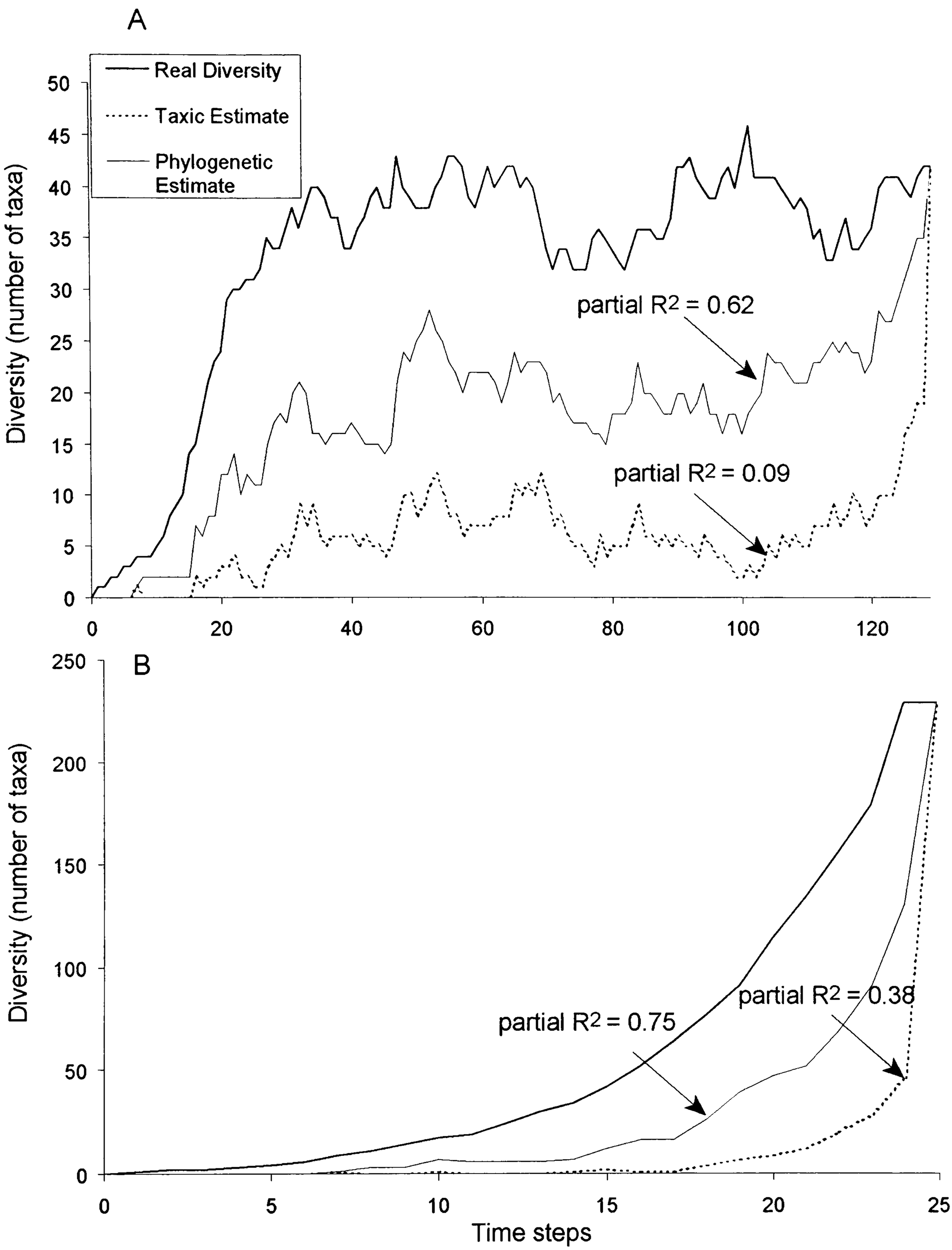


FIGURE 2.10. Examples of the superiority of the phylogenetic method (A) A logistic diversification pattern (B) An exponential diversification pattern. Sampling rate in both is 0.1, demonstrating the ability of the phylogenetic method to recover lost diversity in poorly sampled clades. However, neither analysis includes ancestors in the analysis, nor simulates the Pull of the Recent. The inclusion of both of these conditions reduces the performance of the phylogenetic estimate.

longer defined as singletons for the corrected count. Singletons were included in the diversity counts for all further program runs.

Increasing sampling intensity obviously increases the performance of both methods of estimating diversity, though the increase is far greater in the uncorrected count as sampling rate moves up from 0.1 to 0.5. Similarly, both estimates tend to produce a better performance in analyses of larger clades than those of smaller clades.

2.3.2. GHOSTRANGE_A further investigations

The effect of diversification pattern and Pull of the Recent

A closer examination of the initial results for exponential diversification patterns reveals that taxic estimates of diversity perform as well as or better than the phylogenetic method in the majority of program runs (Table 2.2).

	Parameter value	Taxic diversity		Phylogenetic diversity	
		Mean partial R^2	Mean maximum diversity magnitude (%)	Mean partial R^2	Mean maximum diversity magnitude (%)
Exponential diversification	Small phylogeny	**0.59**	76	**0.61**	**121**
	Large phylogeny	**0.66**	77	**0.66**	**112**
	MEx not included	**0.62**	75	**0.63**	**115**
	MEx included	**0.62**	78	**0.65**	**118**
	SI = 0.1	0.42	67	0.53	94
	SI = 0.5	**0.82**	86	**0.74**	**139**
	PR not included	**0.66**	52	**0.42**	**108**
	PR included	0.58	100	0.84	**125**
	Ancestors not included	0.64	67	0.73	80
	Ancestors included	**0.6**	87	**0.53**	**154**

Table 2.2. Expansion of initial results for simulations of exponential diversification., $n = 64$. For explanation of symbols see Table 2.1.

The taxic method also performs better than the phylogenetic in program runs where 'Pull of the Recent' is not simulated (Table 2.3), i.e. taxa have the same chance of being sampled in the final time interval as they do in all others.

	Parameter value	Taxic diversity		Phylogenetic diversity	
		Mean partial R^2	Mean maximum diversity magnitude (%)	Mean partial R^2	Mean maximum diversity magnitude (%)
No 'Pull of the Recent'	no. taxa ~100	**0.5**	62	**0.54**	**123**
	no. taxa ~ 500	**0.67**	57	**0.63**	**115**
	Exponential	**0.67**	52	**0.42**	**108**
	Logistic	0.51	66	0.74	**129**
	MEx not included	**0.61**	62	**0.6**	**121**
	MEx included	**0.56**	57	**0.57**	**117**
	SI = 0.1	0.41	40	0.47	97
	SI = 0.5	**0.76**	79	**0.69**	**141**
	Ancestors not included	0.56	42	0.68	74
	Ancestors included	**0.61**	77	**0.49**	**164**

Table 2.3. Expansion of initial results for simulations without 'Pull of the Recent', $n = 64$. For explanation of symbols see Table 2.1.

Hence, the most striking examples of taxic estimates out-performing phylogenetic estimates are expected to occur when a combination of an exponential diversification pattern without 'Pull of the Recent' is simulated. To investigate this hypothesis 10 phylogenies were generated using the following parameters:

- Large phylogeny
- Initial origination rate 0.25
- Initial extinction rate 0.05
- Exponential diversification
- Mass extinctions not included.

These phylogenies were then sampled using the parameters below:

- Sampling intensity 0.5
- Pull of the recent not included
- Ancestors included
- Singletons included.

The results are shown in Table 2.4.

Phylogeny file name	No. Lineages	Time steps	Taxic Diversity			Phylogenetic Diversity		
			Maximum diversity magnitude (%)	Minimum diversity magnitude (%)	Partial R^2	Maximum diversity magnitude (%)	Minimum diversity magnitude (%)	Partial R^2
expo1	579	30	100	25	**0.91**	200	48	**0.46**
expo2	561	34	100	16	**0.97**	200	50	**0.63**
expo3	543	31	100	44	**0.91**	200	47	**0.44**
expo4	553	33	100	44	**0.95**	200	51	**0.52**
expo5	569	35	100	37	**0.94**	200	50	**0.55**
expo6	577	33	100	33	**0.93**	200	49	**0.56**
expo7	543	26	100	33	**0.88**	200	44	**0.22**
expo8	545	27	100	42	**0.9**	200	50	**0.34**
expo9	601	41	100	50	**0.97**	200	53	**0.73**
expo10	613	23	100	33	**0.93**	200	50	**0.36**
		Mean:	100	36	**0.93**	200	49	**0.48**

Table 2.4. Exponential diversification simulations with no 'Pull of the Recent'. For explanation of symbols see Table 2.1.

These results confirm that under the limited conditions set out above, taxic diversity counts capture on average over twice as much of the actual diversity pattern as the phylogenetic estimate. Figure 2.11 shows an exponential phylogeny sampled both (A) with and (B) without Pull of the Recent, sampled at a rate of 0.5. Figure 2.12 shows the same phylogeny sampled at a rate of 0.1 (A), and sampled with ancestors included in the analysis (B). The graphs show a difference in pattern between the two estimates. The taxic estimate follows an exponential rise until diversity levels out or drops towards the end. This decrease in diversification is caused by the Signor-Lipps effect (Signor & Lipps, 1982): the drop in sampling seen in the run up to a co-coordinated set of end-of-ranges, such as produced by a mass extinction or in this case the end of the program run. This effect also occurs in taxic studies of a discrete time interval where the sampled ranges of taxa extending beyond the end of the interval are not considered, and is one of the 'edge-effects' identified by Foote (2000a). The phylogenetic estimate displays a 'humped' pattern. At first it rises exponentially mirroring the real data, but towards the termination of the curve it levels out and then drops to converge with the taxic estimate. Hence the phylogenetic estimate appears to exaggerate the Signor-Lipps effect. This is not seen when 100% sampling in the final time interval is imposed as this eliminates unsampled end-of-range from the crown taxa.

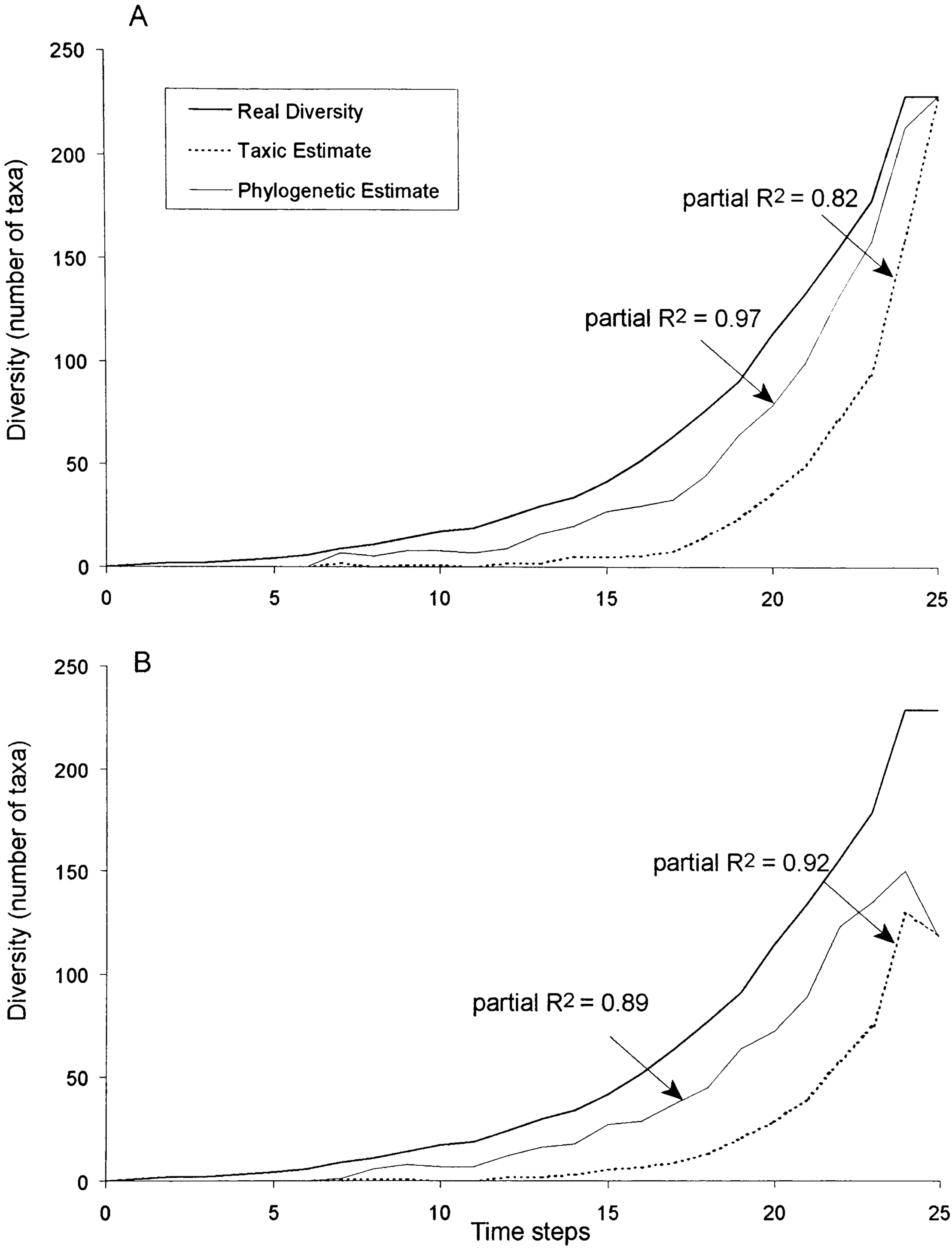


FIGURE 2.11. Exponential diversification patterns, sampling rate 0.5 (A) With 'Pull of the Recent' simulated the phylogenetic estimate out-performs the taxic (B) Without 'Pull of the Recent' simulated the taxic estimate performs best. The decrease in diversity at the end of both estimated diversity curves is due to the 'Signor-Lipps' sampling effect seen prior to a cluster of last appearances - in this case the end of the program run. The phylogenetic estimate exaggerates this effect giving the diversity curve a 'humped' look.

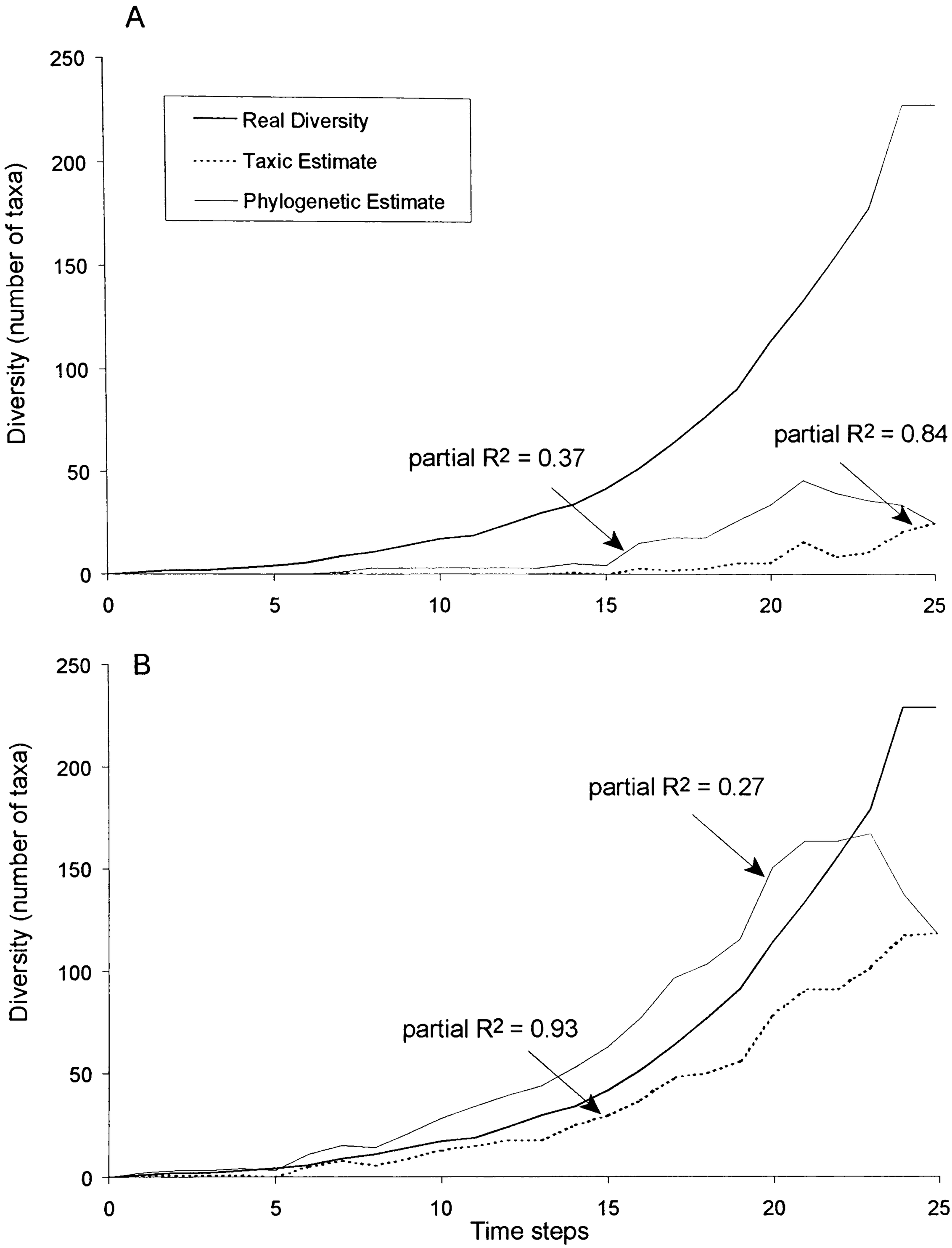


FIGURE 2.12. Exponential diversification patterns without 'Pull of the Recent' simulated. (A) Sampling rate 0.1. Despite capturing very little diversity magnitude, the taxic estimate still significantly out-performs the phylogenetic at capturing the diversity pattern (B) Sampling rate 0.5, ancestors included in analysis and misdiagnosed as sister taxa. Again under these conditions the phylogenetic estimate performs very poorly due to the large skew in diversity apparent at the end of the curve.

Therefore the phylogenetic method of assessing biodiversity is less accurate than the taxic count in situations where a clade had diversified exponentially, and where there is no reason to assume perfect sampling in the final time interval. This is the case either where an extant clade is believed to be poorly sampled in the Recent, or when the final time step is not the Recent (e.g. where only part of the diversification of a clade is assessed, or the clade has become extinct).

The decrease in diversity level towards the end of the time period is also evident in both the taxic and phylogenetic estimates of logistic diversification (Fig. 2.13), although it is likewise more pronounced in the phylogenetic. This skew does not alter the phylogenetic pattern to the same extent as in exponential diversification, and in most cases the corrected count performs better than the uncorrected under conditions of logistic growth.

Ancestors mistaken as sister species

The results of the initial analysis for program runs including misdiagnosed ancestral taxa are expanded in Table 2.5.

	Parameter value	Uncorrected diversity		Corrected diversity	
		Mean partial R^2	Mean maximum diversity magnitude (%)	Mean partial R^2	Mean maximum diversity magnitude (%)
Ancestors Included in analysis	No. taxa ~ 100	0.52	89	0.62	**166**
	No. taxa ~ 500	**0.64**	88	**0.69**	**155**
	MEx not included	0.57	87	0.63	**157**
	MEx included	0.59	90	0.68	**164**
	Exponential	**0.6**	87	**0.53**	**154**
	Logistic	0.56	91	0.78	**168**
	SI = 0.1	0.34	79	0.58	**132**
	SI = 0.5	**0.81**	97	**0.73**	**189**
	PR not included	**0.61**	77	**0.49**	**164**
	PR included	0.55	100	0.82	**157**

Table 2.5. Expansion of initial results for simulations with misdiagnosed ancestors, $n = 64$. For explanation of symbols see Table 2.1.

Once again where an exponential diversification pattern is used without imposing Pull of the Recent, the taxic count out-performs the phylogenetic. When sampling

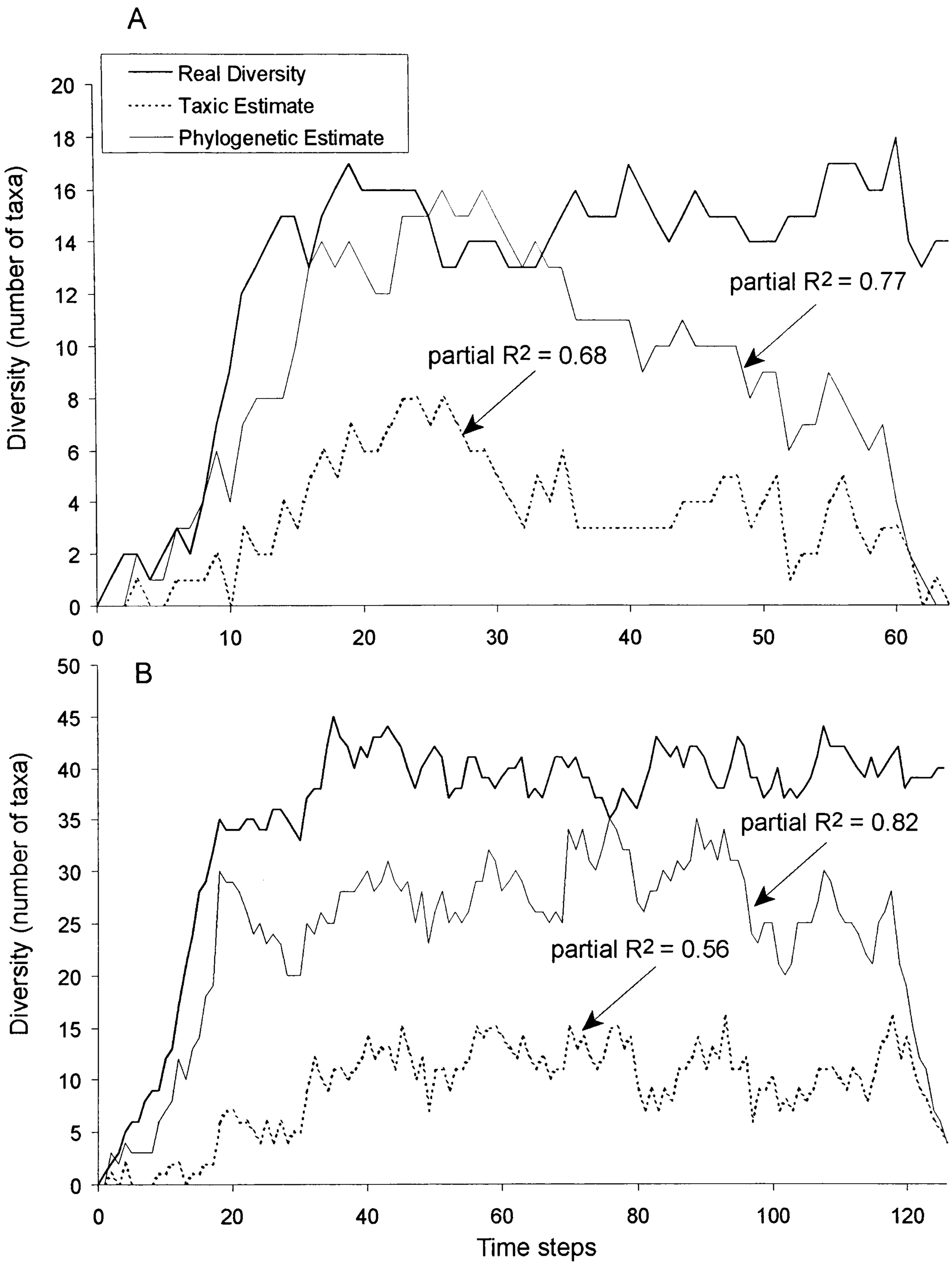


FIGURE 2.13. Logistic diversification patterns without 'Pull of the Recent' simulated (A) Small phylogeny, sampling rate 0.1, ancestors included and misdiagnosed. (B) Large phylogeny, sampling rate 0.1, ancestors included and misdiagnosed. The downwards skew in diversity at the end of the curve caused by the Signor-Lipps sampling effect is evident in both estimates, though it is more pronounced in the phylogenetic. However, unlike that seen in exponential diversification patterns the skew is not enough to reduce the performance of the phylogenetic estimate below that of the taxic.

intensity is high and ancestors are mistaken for sister taxa, the taxic count also performs as well as or better than the phylogenetic. To investigate this further 20 phylogenies were produced, (10 small, 10 large) using the following parameters:

- Initial origination rate 0.25
- Initial extinction rate 0.05
- Logistic diversification
- Mass extinctions not included.

These 20 were then sampled twice each, once with Pull of the Recent simulated and once without, using the following sampling parameters:

- Sampling intensity 0.5
- Ancestors included
- Singletons included.

This results in 10 experiments of identical parameters, performed both on large and small clades, with and without Pull of the Recent. The results are shown in Table 2.6.

Clade size	Pull of the Recent	Taxic Diversity			Phylogenetic Diversity		
		Mean maximum diversity magnitude (%)	Mean minimum diversity magnitude (%)	Mean partial R^2	Mean maximum diversity magnitude (%)	Mean minimum diversity magnitude (%)	Mean partial R^2
Small	Y	100	37	0.63	**198**	82	0.76
Small	N	100	34	**0.66**	**200**	46	**0.66**
Large	Y	100	38	**0.95**	**194**	79	**0.96**
Large	N	100	31	**0.93**	**198**	51	**0.94**

Table 2.6. Simulations with misdiagnosed ancestors and high sampling intensity, $n = 10$. For explanation of symbols see Table 2.1.

The above results confirm that in situations of good sampling, where misdiagnosed ancestors are included in the addition of ghost ranges, the taxic count performs as well as the corrected if there is no Pull of the Recent. In large clades the performances are equal when Pull of the Recent is simulated. In addition the maximum diversity magnitude estimates for the corrected count are up to 200% more than the

actual values. This large over-estimation is produced by the addition of ghost taxa between ancestors and descendents (Fig. 2.14). If sampling is poor, the performance of both estimates falls but not necessarily by the same amount. A small phylogeny was generated using a logistic diversification pattern, and then sampled 20 times at a low rate of 0.1 fossil occurrences per time interval. Ancestors have been included in the analysis, and no Pull of the Recent was simulated. The resulting mean time de-trended correlation values are shown in Table 2.7.

	Taxic diversity mean partial R^2	**Phylogenetic diversity mean partial R^2**
Ancestors included, SI = 0.1	0.46	0.64

Table 2.7 Simulations with misdiagnosed ancestors and low sampling intensity, $n = 20$. For explanation of symbols see Table 2.1.

Comparison with the results for small clades in Table 2.6 shows that a lower sampling intensity has little effect on the phylogenetic estimate when ancestors are included in the analysis, only a small drop in its performance is evident. Conversely, the performance of the taxic estimate is significantly reduced. This is due to the large loss of information in the taxic method that results from a low sampling rate.

Mass extinctions

An expansion of the initial analysis results for mass extinctions is shown in Table 2.8. Simulations including mass extinctions produce similar results to those excluding them; i.e. the only situations in which the taxic count matches the phylogenetic are those with an exponential diversification pattern and incomplete sampling in the final time interval. If ancestors are included in the analysis the taxic count increases in performance and the phylogenetic decreases. Examples are shown in Figure 2.15.

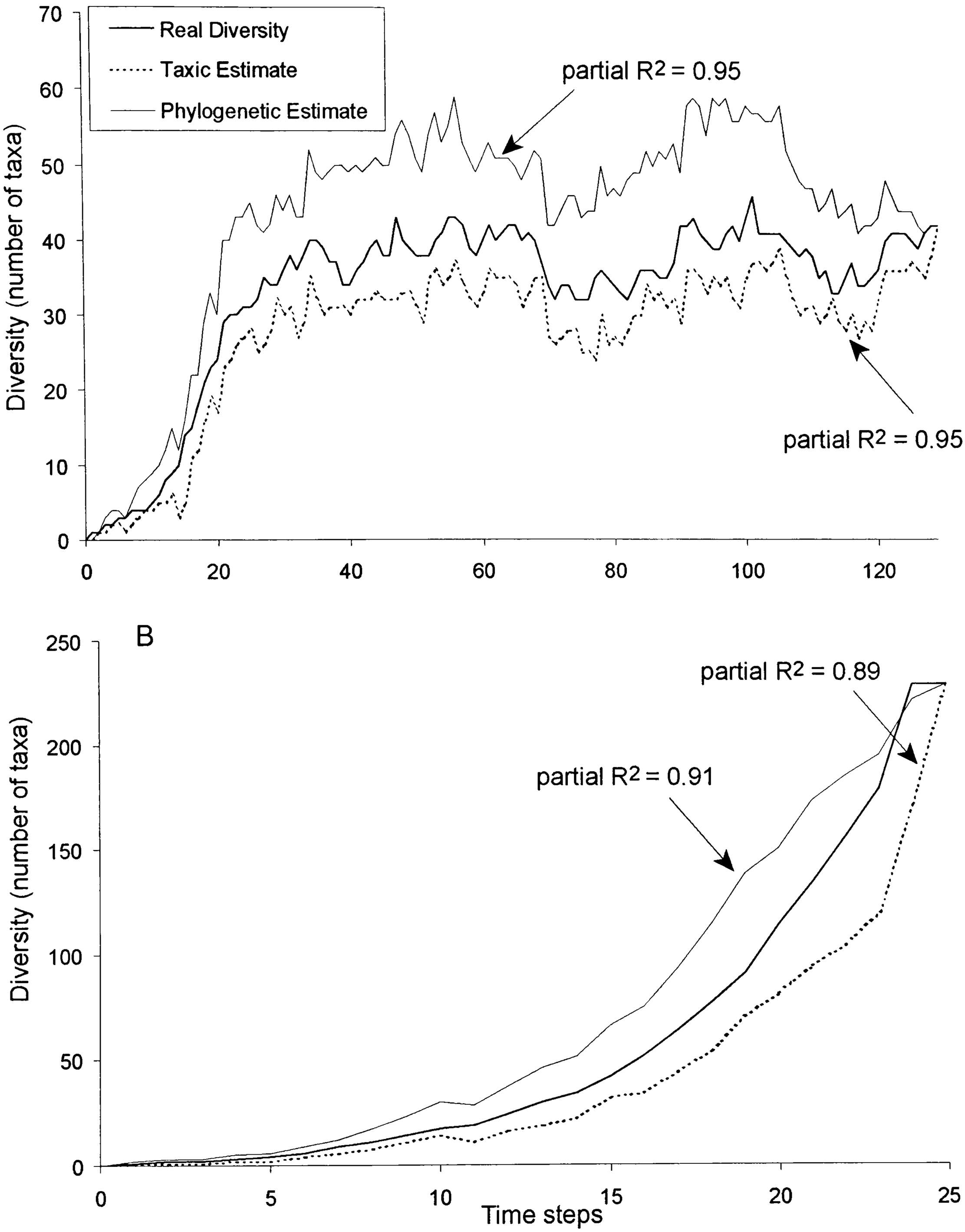


FIGURE 2.14. Ancestors sampled but misdiagnosed as sister taxa of their descendent groups. Sampling rate 0.5. (A) Logistic diversification. (B) Exponential diversification. In each case the performance of both estimates is high. However, the phylogenetic estimate significantly and consistently over-estimates diversity magnitude through the history of the clade.

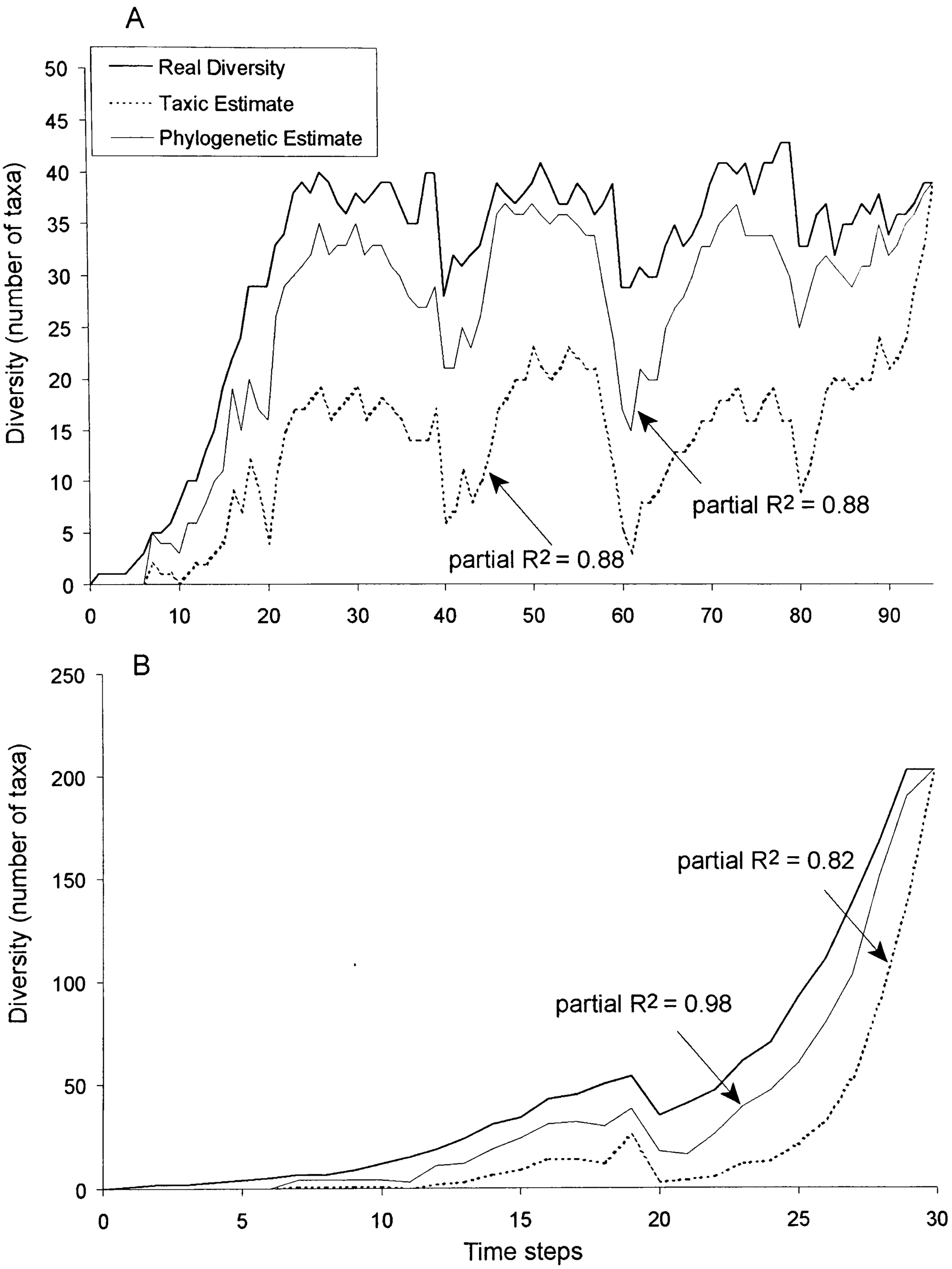


FIGURE 2.15. The effect of mass extinctions. Sampling rate 0.5, 'Pull of the Recent' included, mass extinctions simulated every 20 time steps. (A) Logistic diversification. (B) Exponential diversification. In each case the phylogenetic estimate out-performs the taxic, regardless of mass extinction events.

	Parameter value	Taxic diversity		Phylogenetic diversity	
		Mean partial R^2	Mean maximum diversity magnitude (%)	Mean partial R^2	Mean maximum diversity magnitude (%)
Mass Extinctions included	No. taxa ~ 100	0.47	100	0.63	**198**
	No. taxa ~ 500	0.56	77	0.7	**119**
	Exponential	**0.62**	75	**0.63**	**115**
	Logistic	0.41	82	0.7	**129**
	SI = 0.1	0.31	69	0.55	**102**
	SI = 0.5	0.72	88	0.78	**143**
	Ancestors not included	0.47	70	0.7	87
	Ancestors included	0.57	87	0.63	**157**
	PR not included	**0.56**	57	**0.57**	**117**
	PR included	0.47	100	0.76	**127**

Table 2.8. Expansion of initial results for simulations with mass extinction events, $n = 64$. For explanation of symbols see Table 2.1.

To further investigate the performance of both diversity estimates around mass extinction events, 20 large, logistic phylogenies were generated, 10 with mass extinctions and 10 without. All phylogenies were sampled at a probability of 0.5 occurrences per time interval, with no Pull of the Recent and excluding ancestors. The results are shown in Table 2.9.

	Taxic diversity mean partial R^2	Phylogenetic diversity mean partial R^2
Mass extinctions included	0.68	0.89
Mass extinctions excluded	0.68	0.94

Table 2.9. Logistic diversification simulations with and without mass extinctions. Mean correlation values are shown for each estimate, $n = 10$.

The corrected diversity count performs consistently better than the uncorrected, indicating that mass extinction events do not adversely effect the phylogenetic method if ancestral taxa are excluded. To investigate the combined effect of mass extinctions and misdiagnosed ancestral taxa, a further 10 phylogenies were generated with the same

parameters as those in Table 2.9, each was sampled twice, once with and once without ancestors.

	Taxic diversity mean partial R^2	Phylogenetic diversity mean partial R^2
Ancestors included	**0.84**	**0.8**
Ancestors excluded	0.67	0.88

Table 2.10. Simulations including mass extinctions, with and without misdiagnosed ancestors. Mean correlation values are shown for each estimate, *n* = 10.

The results in Table 2.10 demonstrate that when a clade is affected by mass extinctions, and if sampled ancestral taxa are misdiagnosed as sister taxa, the taxic count performs as well as the phylogenetic method at reproducing diversity pattern (Fig 2.16). How well do the two estimates capture the magnitude of mass extinction events? The 10 phylogenies generated above were analysed to calculate the percentage loss of taxa during each mass extinction event. The corresponding magnitude loss was also calculated for the two diversity estimates. Each percentage loss was calculated only for the time step in which the extinction event occurred and provides a comparison with the standing diversity of the time step before. The mean results are shown in Table 2.11.

	Actual data	Taxic estimate	Phylogenetic estimate
Mean % loss of taxa	46.4	44.8	25.6

Table 2.11. Magnitude of mass extinction events in simulated data sets. Measurements given as mean percentage taxonomic loss, *n* = 62.

Within the time step of the extinction event, the corrected estimate considerably underestimates the percentage taxonomic loss, while the taxic count captures the event more accurately. However examination of the diversity curves containing mass extinction events demonstrate that the phylogenetic estimate does capture the magnitude

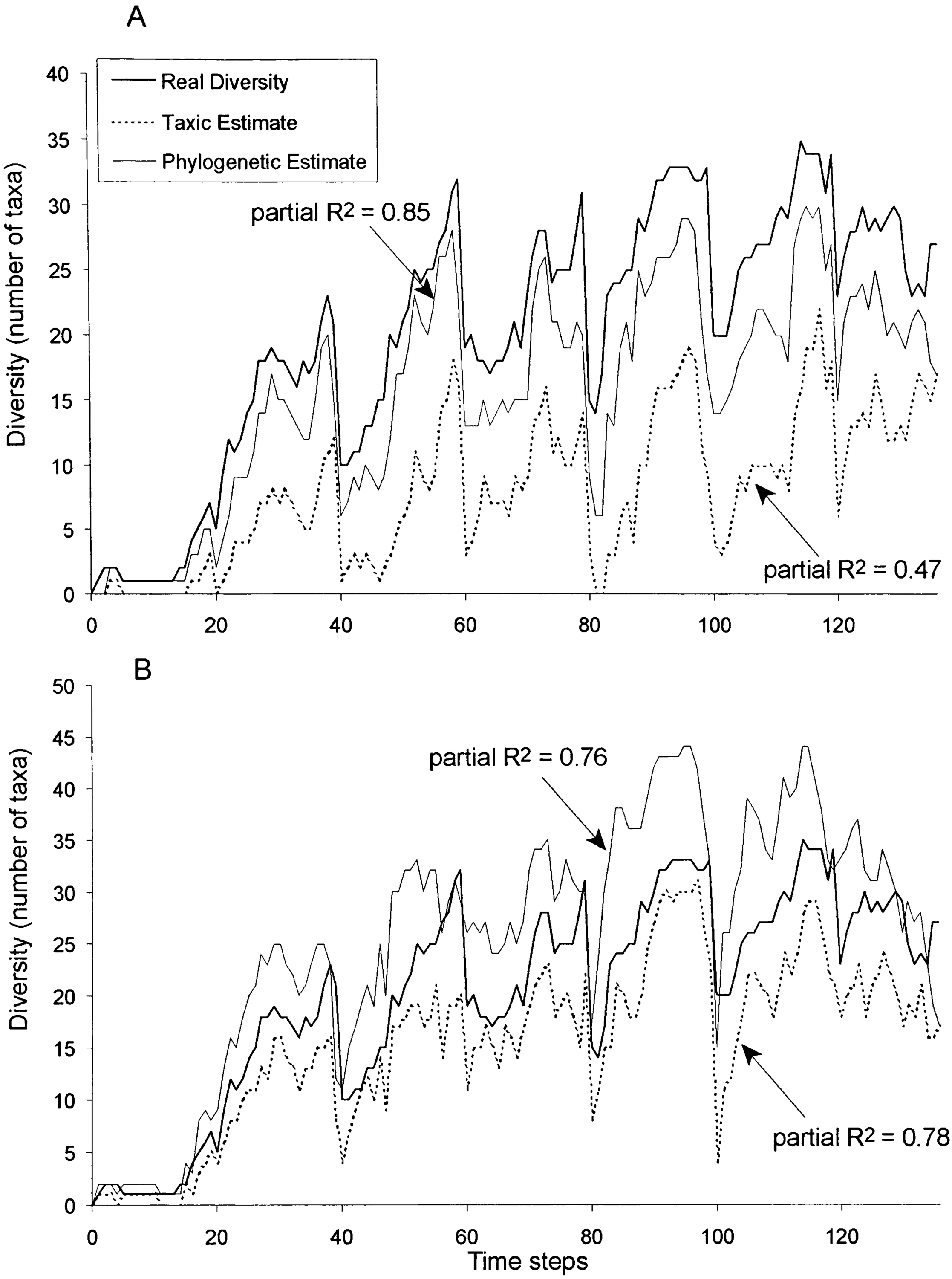


FIGURE 2.16. Mass extinctions in phylogenies with, and without, sampled ancestors. (A) Ancestors not included in the analysis. (B) Ancestors included in the analysis and misdiagnosed as sister taxa of their descendent groups. The combination of mass extinctions and misdiagnosed ancestors reduces the performance of the phylogenetic estimate to below that of the taxic method.

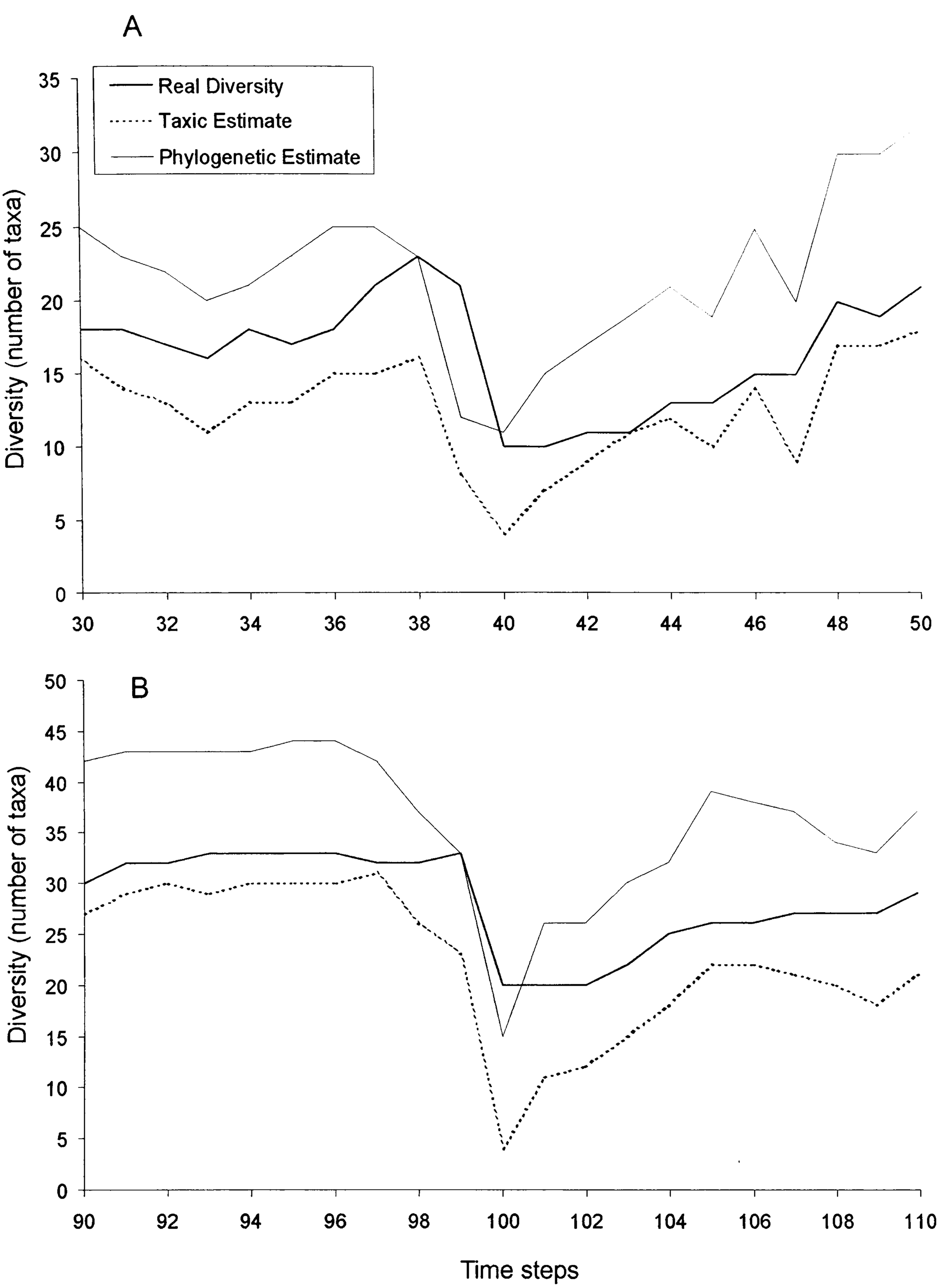


FIGURE 2.17. Detail of two of the mass extinction events evident in Fig. 15B. (A) Extinction event at 40 time steps. The phylogentic estimate captures the magnitude of the loss of taxa, but prolonged over a greater number of time steps than that of the event. (B) Extinction event at 100 time steps. Both estimates display a greater loss of diversity than in reality, and both show a diversity drop prior to the event, the decrease in the taxic estimate starting at time step 97 and in the phylogenetic estimate at time step 96.

of taxonomic loss, but prolonged over a greater number of time steps (Fig. 2.17). The simple taxic count smears the mass extinction events to a certain degree, but the phylogenetic estimate exaggerates this causing the diversity fall-off prior to a mass extinction to start earlier in the time sequence. As an example, in Figure 2.17A the actual mass extinction event involves a 52% loss of diversity over one time step, the uncorrected estimate gives a 75% loss over two time steps, and the corrected count gives a 56% loss over three time steps. Therefore the corrected count provides a more accurate estimate of extinction magnitude, but prolonged over a longer time length.

2.3.3. GHOSTRANGE_B analysis

To provide an unbiased test of the phylogenetic estimate, the GHOSTRANGE_B version of the program was used to simulate phylogenies where ancestors, if sampled, were recognised as such, and ghost lineages correctly inserted (cf. Smith 1994 and see Section 2.2.2.3). 256 program runs were performed using an origination rate of 0.25 and an extinction rate of 0.05. All combinations of parameters were run, both with and without singletons included in diversity counts. The results are shown in Table 2.12.

	Parameter value	Taxic diversity mean partial R^2	Phylogenetic diversity mean partial R^2
Small clades	Exponential	0.4	0.48
	Logistic	0.37	0.63
	MEx not included	0.46	0.66
	MEx included	0.29	0.45
	SI = 0.1	0.17	0.39
	SI = 0.5	0.59	0.72
	PR not included	**0.37**	**0.42**
	PR included	0.38	0.69
Large clades	Exponential	**0.67**	**0.7**
	Logistic	0.64	0.85
	MEx not included	0.73	0.82
	MEx included	0.58	0.72
	SI = 0.1	0.42	0.63
	SI = 0.5	**0.89**	**0.92**
	PR not included	**0.72**	**0.67**
	PR included	0.59	0.88

Table 2.12. Summary of results from 256 runs of GHOSTRANGE_B program. Ancestors are sampled, correctly diagnosed, and ghost lineages inserted accordingly. Data shown are mean values for all runs incorporating the stated

parameter on either small or large phylogenies; *n* in each case is 64. For explanation of symbols see Table 2.1.

Once again the phylogenetic method is superior to the taxic in the majority of simulations. The two are only comparable in situations of high sampling rate, exponential diversification and when 'Pull of the Recent' is not simulated. However, these last two conditions do not raise the performance of the taxic estimate above that of the phylogenetic to the same extent as when ancestors are misdiagnosed (See Table 2.1).

To summarize and compare the results obtained from both versions of the GHOSTRANGE program, mean correlation values for the taxic and phylogenetic estimates have been extracted from Table 2.1, both in simulations where ancestors were not sampled, and those where they were sampled but misdiagnosed. Similarly, mean correlation values for the phylogenetic estimate, in simulations where ancestors were sampled and correctly diagnosed, were calculated from the data summarised in Table 2.12 above. These mean values are shown in Table 2.13 for both small and large clades.

	Taxic estimate mean partial R^2		Phylogenetic estimate mean partial R^2		
	Ancestors not sampled	**Ancestors sampled**	**Ancestors not sampled**	**Ancestors sampled and misdiagnosed**	**Ancestors sampled and correctly diagnosed**
Small clades	0.42	0.52	0.65	0.62	0.56
Large clades	0.55	0.64	0.78	0.69	0.77

Table 2.13. Mean correlation results for all three methods of dealing with ancestors, *n*= 64.

The mean correlation values in Table 2.13 demonstrate that on average the phylogenetic method out-performs the taxic under all conditions of ancestor sampling and diagnosis. If a phylogeny does contain sampled ancestors, however, the performance of the phylogenetic estimate is reduced irrespective of their correct diagnosis, although this reduction is only minor in large clades. In fact, the phylogenetic estimate captures more of the real diversity pattern in small clades when ancestors are incorrectly identified. The correct diagnosis of ancestors reduces the over-estimation of

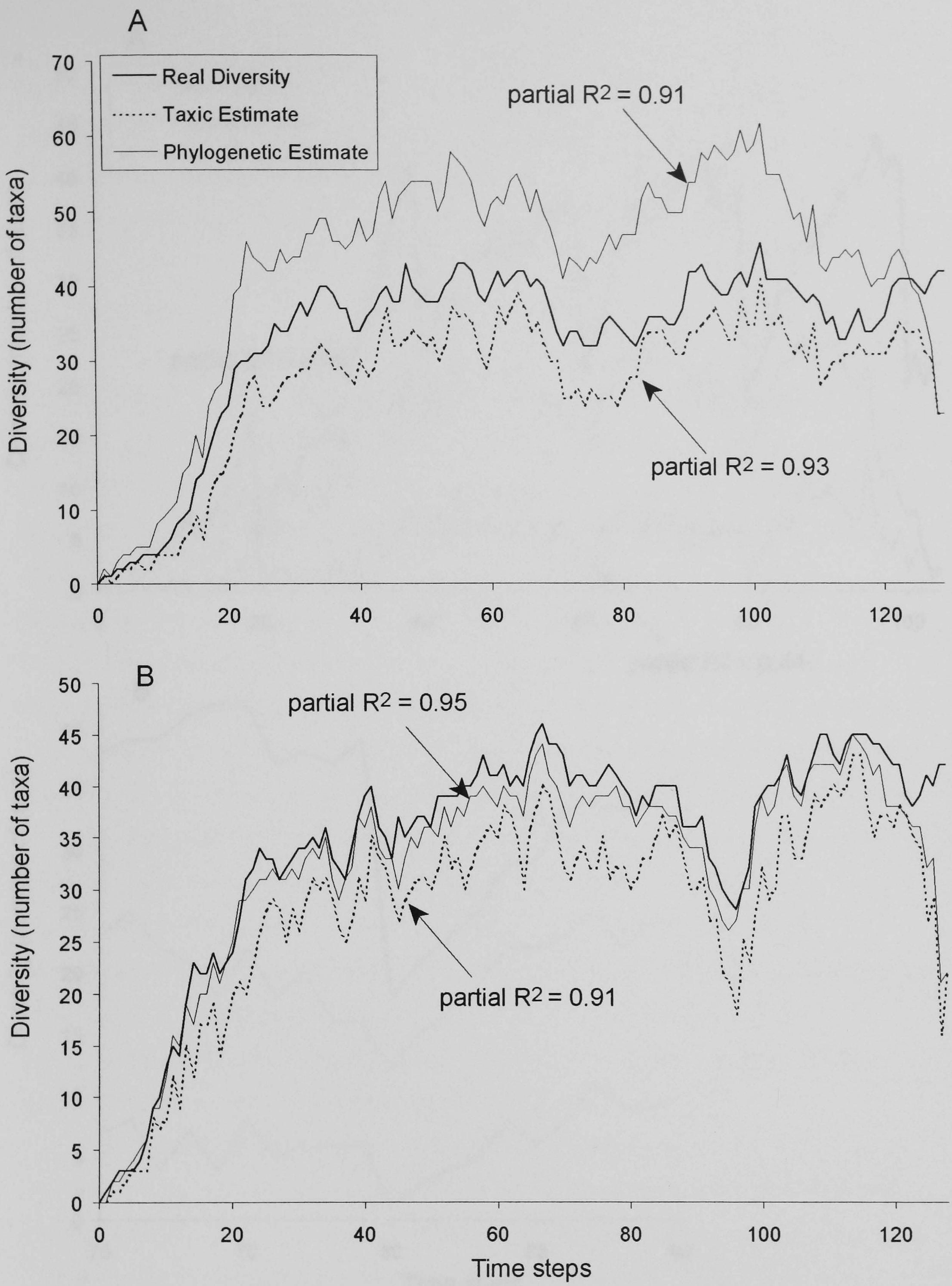


FIGURE 2.18. The effect of misdiagnosing ancestors. Sampling rate = 0.5. (A) If ancestors are mistaken as the sister taxa of their descendent groups, the unnecessary addition of ghost lineages causes the phylogenetic estimate to overestimate diversity levels. (B) If ancestors are correctly diagnosed and ghost lineages inserted correctly (cf Smith 1994) the diversity magnitude estimate is more reasonable.

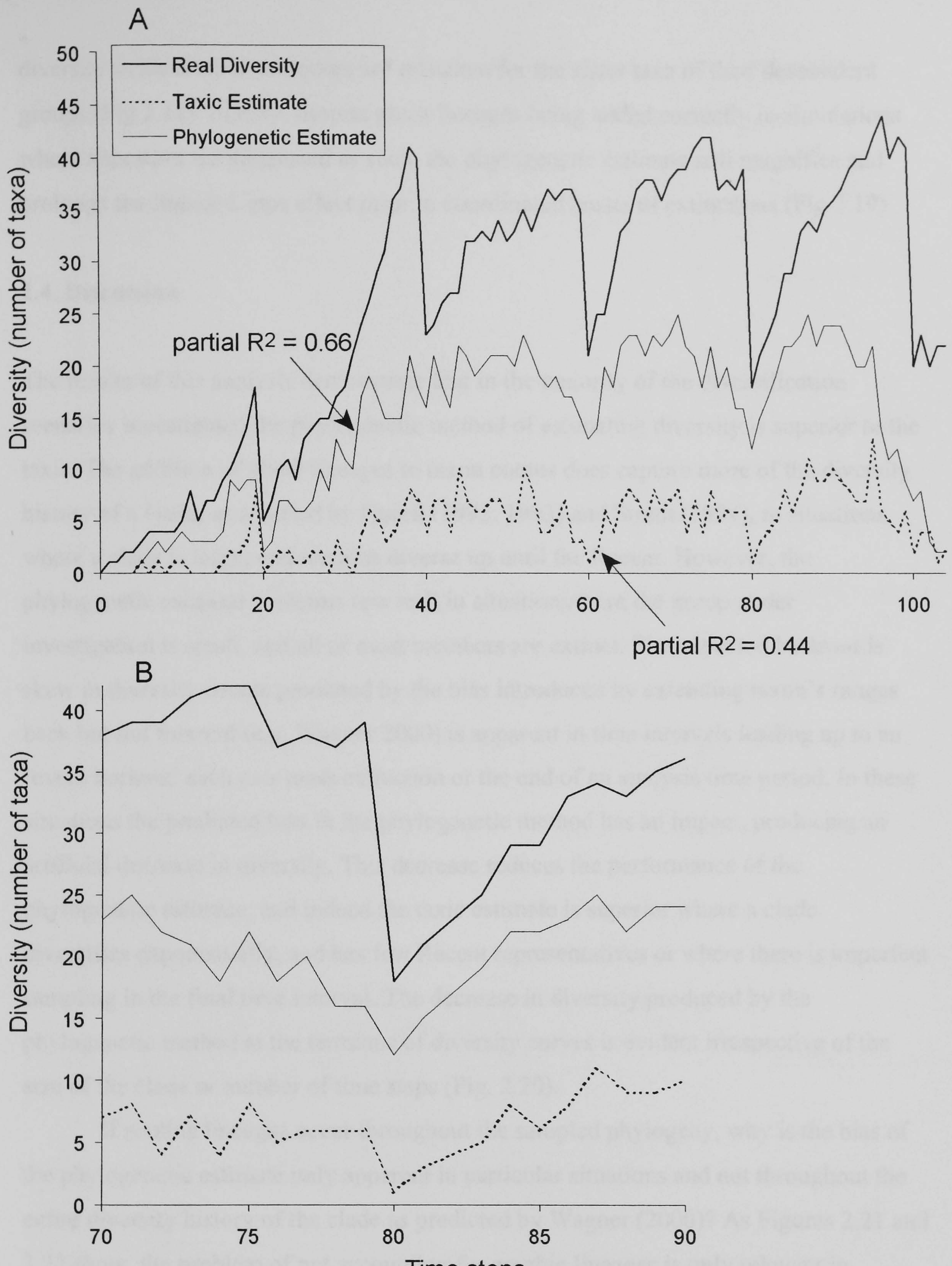


FIGURE 2.19. Mass extinctions with ancestors correctly identified (A) Sampling rate = 0.1. The phylogenetic estimate smears extinction events backward making them appear gradual rather than catastrophic. (B) Detail of extinction event at 80 time steps. A 52% loss over one time step in the complete diversity curve results in a 54% loss over nine time steps using the phylognetic estimate. The taxic estimate produces a 88% loss over five time steps, however this is an unrealiable figure due to the low diversity level of the taxic count.

diversity evident when ancestors are mistaken for the sister taxa of their descendent groups (Fig 2.18). Finally, despite ghost lineages being added correctly in simulations where ancestors are diagnosed as such, the phylogenetic estimate still magnifies and prolongs the Signor-Lipps effect prior to coordinated bursts of extinctions (Fig 2.19).

2.4. Discussion

The results of this analysis demonstrate that in the majority of the diversification scenarios investigated the phylogenetic method of estimating diversity is superior to the taxic. The addition of ghost lineages to taxon counts does capture more of the diversity history of a clade, as asserted by Norell (1992, 1993) and Smith (1994), in situations where a clade is large, and remains diverse up until the Recent. However, the phylogenetic estimate performs less well in situations were the group under investigation is small, and all or most members are extinct. The expected backwards skew in diversity counts predicted by the bias introduced by extending taxon's ranges back but not forward (e.g. Wagner 2000) is apparent in time intervals leading up to an 'event horizon' such as a mass extinction or the end of an analysis time period. In these situations the predicted bias in the phylogenetic method has an impact, producing an artificial decrease in diversity. This decrease reduces the performance of the phylogenetic estimate, and indeed the taxic estimate is superior where a clade diversifies exponentially, and has few Recent representatives or where there is imperfect sampling in the final time interval. The decrease in diversity produced by the phylogenetic method at the terminus of diversity curves is evident irrespective of the size of the clade or number of time steps (Fig. 2.20).

If zombie lineages occur throughout the sampled phylogeny, why is the bias of the phylogenetic estimate only apparent in particular situations and not throughout the entire diversity history of the clade as predicted by Wagner (2000)? As Figures 2.21 and 2.22 show, the problem of not accounting for zombie lineages is only relevant in situations where there is a high proportion of terminal taxa zombie lineages as compared to ghost and sampled range. If the amount of unsampled early and late range is uniformly spread throughout the phylogeny the addition of ghost lineages will raise the diversity count in each time step, but will not skew the diversity pattern. In an idealised clade, constructed and sampled to produce a uniform distribution of ghost lineages as compared to zombie lineages, the addition of ghost lineages produces a

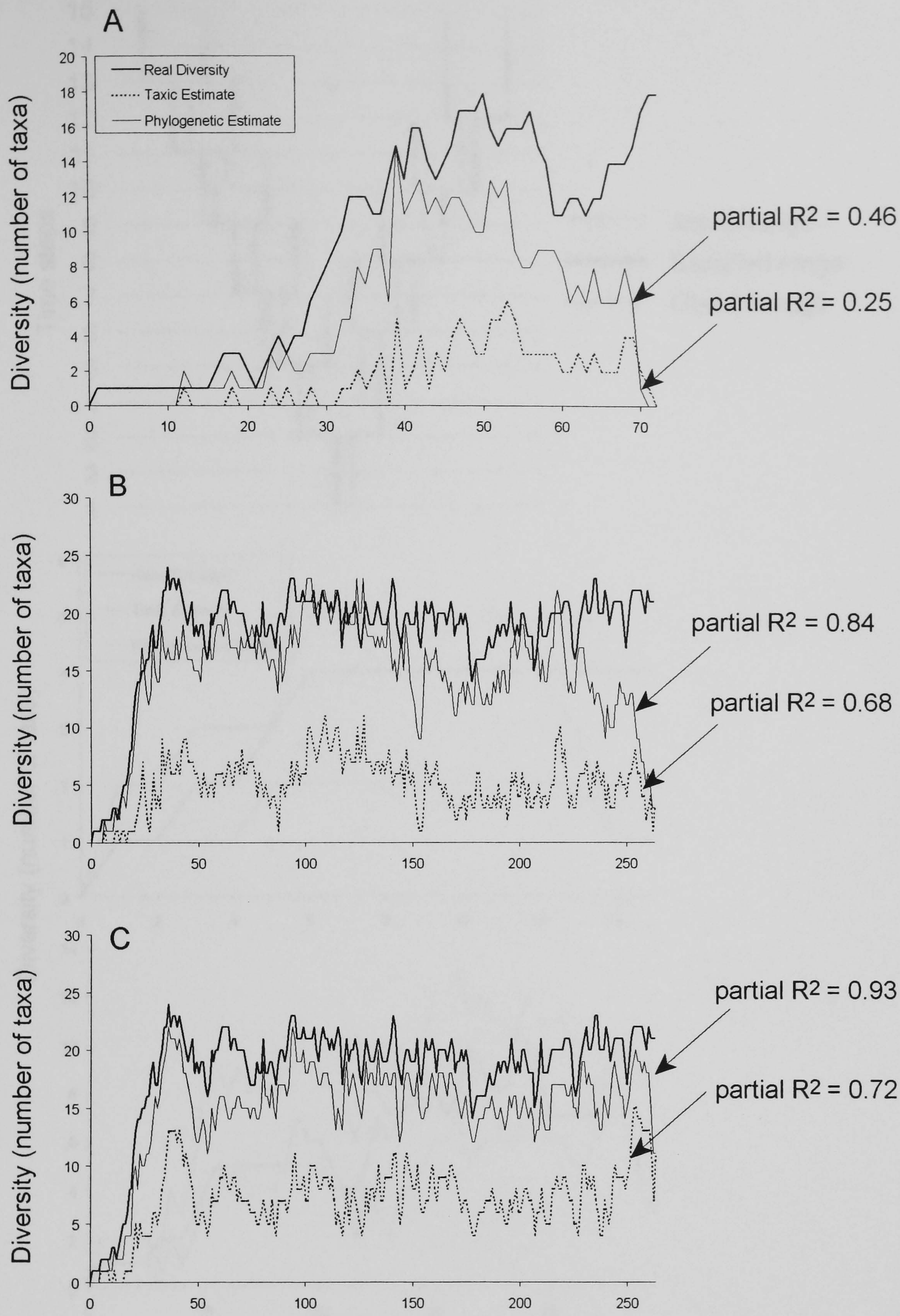


FIGURE 2.20. The predicted bias of the phylogenetic estimate. Diversity skew occurs at the termination of a curve when phylogenetic diversity shows a greater decrease than either the real or the taxic estimate. (A) In a small phylogeny this skew is enough to give the entire curve a humped shape. (B) In a large phylogeny the skew has less impact, only occuring at the termination of the clade's history. (C) If ancestors are not included in the sample a significant terminal diversity decrease is not apparent. The taxic estimate increases towards the termination of the curve as more terminal taxa are available for sampling. The phylogenetic estimate remains more stable due to the dampening effects of the terminal increase in zombie lineages.

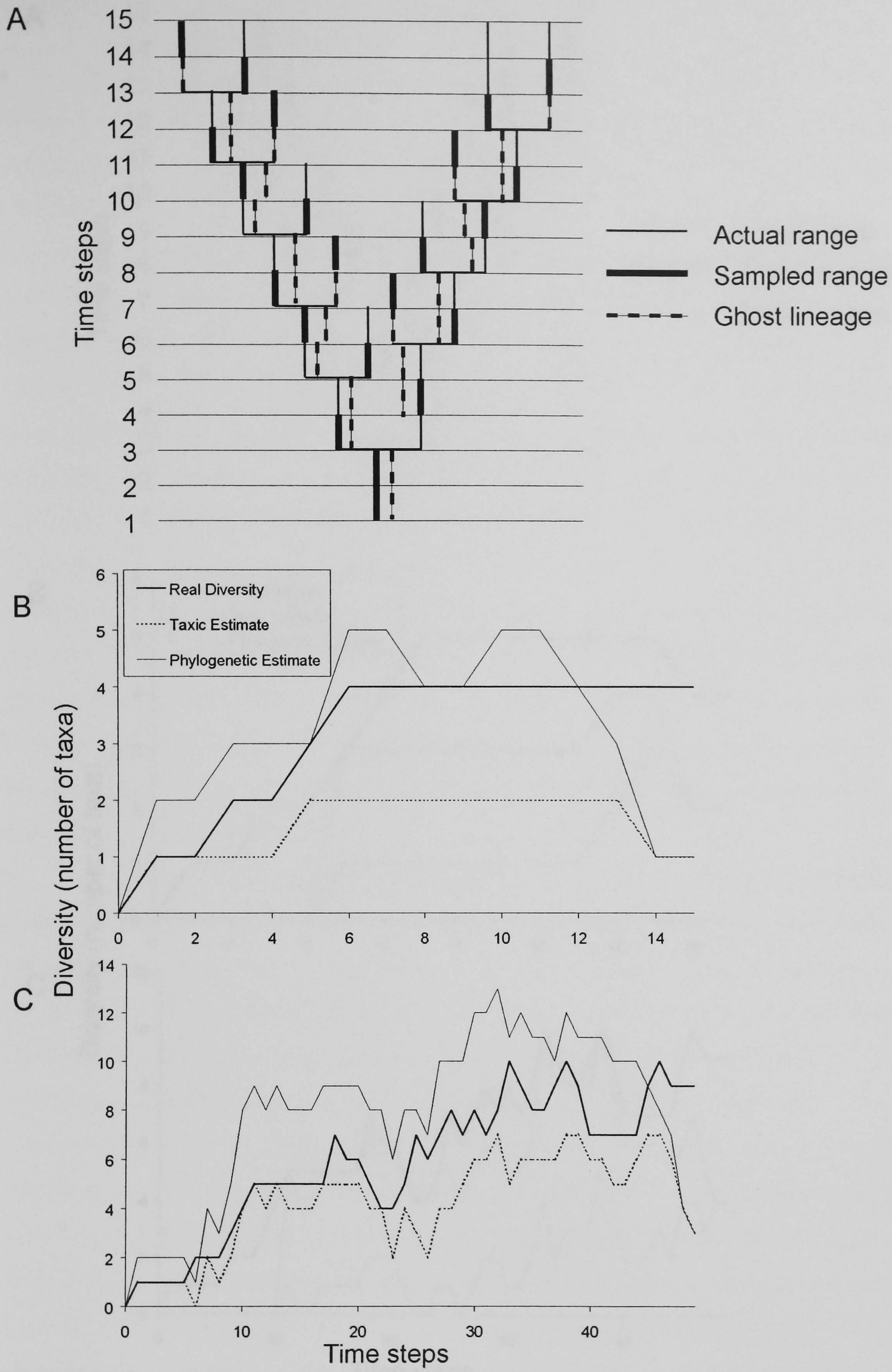


FIGURE 2.21. No long term skew in diversity estimates. (A) An idealised clade is sampled uniformly to produce an even and equal distribution of ghost and zombie lineages. Ghost lineages are inserted assuming that ancestors are misdiagnosed as sister species of their descendent groups. (B) The resulting diversity curves show that the phylogenetic estimate matches the real diversity pattern, with some fluctuations and over-estimation due to the misdiagnosis of ancestors. The only skew in the estimate occurs at the end of the clade's history. It is at this point that the ratio of terminal taxa zombie lineage compared to ancestral zombie lineage increases, so biasing the phylogenetic method. (C) A graph from a program run mirrors the idealised example.

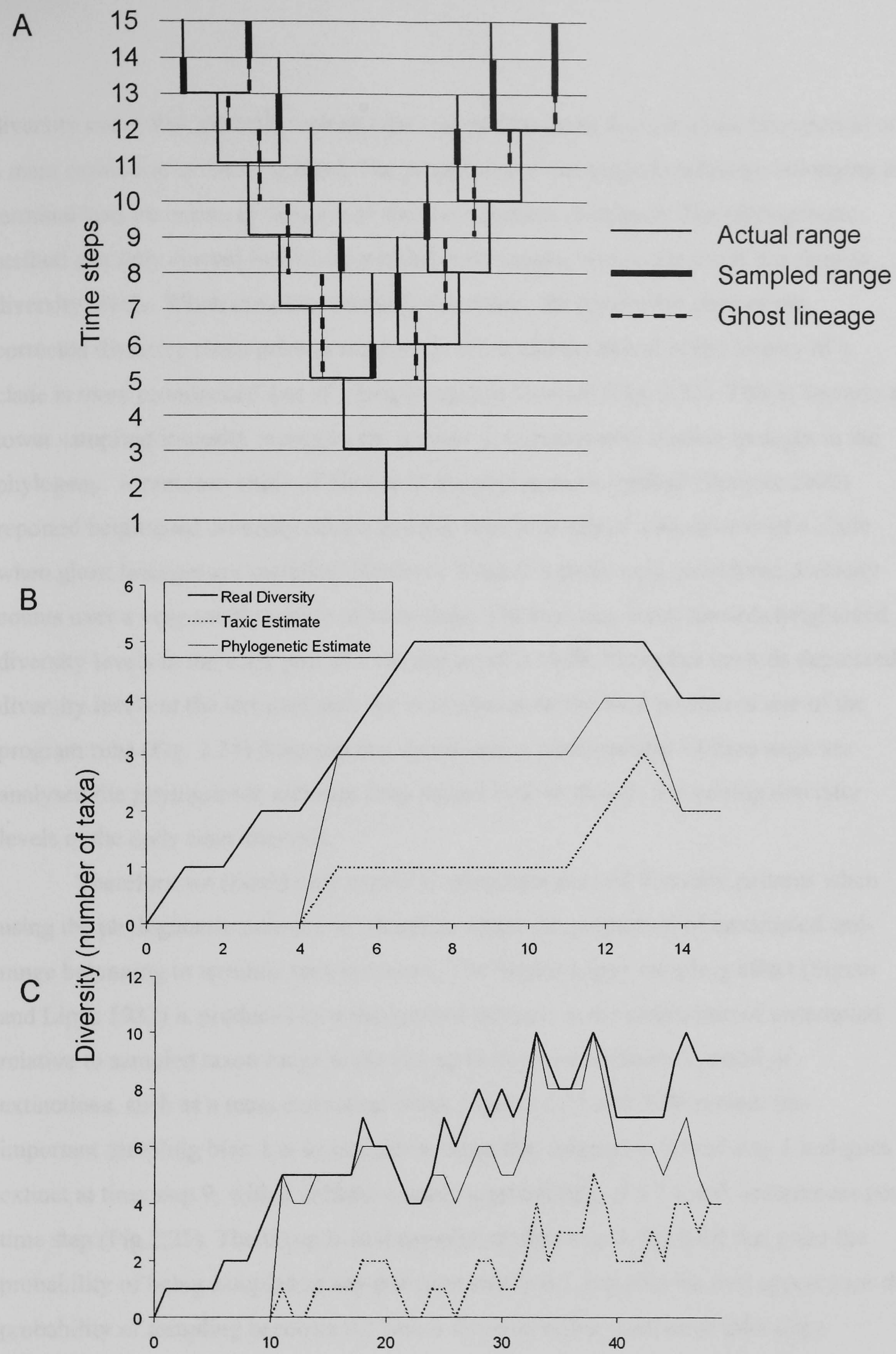


FIGURE 2.22. Less diversity skew without ancestors. (A) An idealised clade is sampled uniformly to produce an even and equal distribution of ghost and zombie lineages; ancestors are not permitted to be found. Ghost lineages are inserted accordingly. (B) The resulting diversity curves show again that the phylogenetic estimate only displays a slight backwards diversity skew. This is because the ratio of terminal taxa zombie lineages compared to ancestral zombie linages is not increasing as ancestors are excluded. Both estimates increase tslightly towards the termination of the curve due to the increased number of terminal taxa available for sampling. (C) A graph from a program run mirrors the idealised example.

diversity count that generally mirrors the real pattern, until the end of the time period or a mass extinction event is reached. The proportion of unsampled end-range belonging to terminal taxa increases as distance to the event horizon decreases. The phylogenetic method can only correct for the unsampled early ranges, and so the result is a drop in diversity levels. When sampling intensity decreases, the downward slant of the corrected diversity count prior to mass extinctions and the at end of the history of a clade is more pronounced and of a longer relative duration (Fig. 2.23). This is because a lower sampling intensity increases the amount of terminal-taxa zombie lineages in the phylogeny. A previous study of the use of the phylogenetic method (Wagner 2000) reported heightened diversity counts in early time intervals of a the history of a clade when ghost lineages are included. However Wagner's study only considered diversity counts over a very small number of time-steps. The real bias is not towards heightened diversity levels in the early part of a the history of a clade, but rather towards depressed diversity levels at the terminal end. An examination of the final portion of one of the program runs (Fig. 2.24) demonstrates that if only a small number of time steps are analysed the phylogenetic estimate does indeed look as though it is raising diversity levels in the early time intervals.

Therefore we should only expect to encounter skewed diversity patterns when using the phylogenetic estimate in situations where the proportion of unsampled end-range belonging to terminal taxa increases. The Signor-Lipps sampling effect (Signor and Lipps 1982) is produced by a the gradual increase in the proportion of unsampled relative to sampled taxon range in the run up to any co-coordinated period of extinctions, such as a mass extinction event. Figures 2.25 and 2.26 explain this important sampling bias. Let us imagine a taxon that originates at time step 1 and goes extinct at time step 9, with a uniform sampling probability of 0.1 fossil occurrences per time step (Fig 2.25). The taxon is first sampled at time step 3. Up until this point the probability of being sampled in any one time step is 0.1, but after its first appearance the probability of sampling becomes 0.1 plus a function of the number of time steps remaining until extinction. This is because the longer the range of a taxon, the more chance there is that it will be sampled at some point in the future, and so filling in the intermediate range.

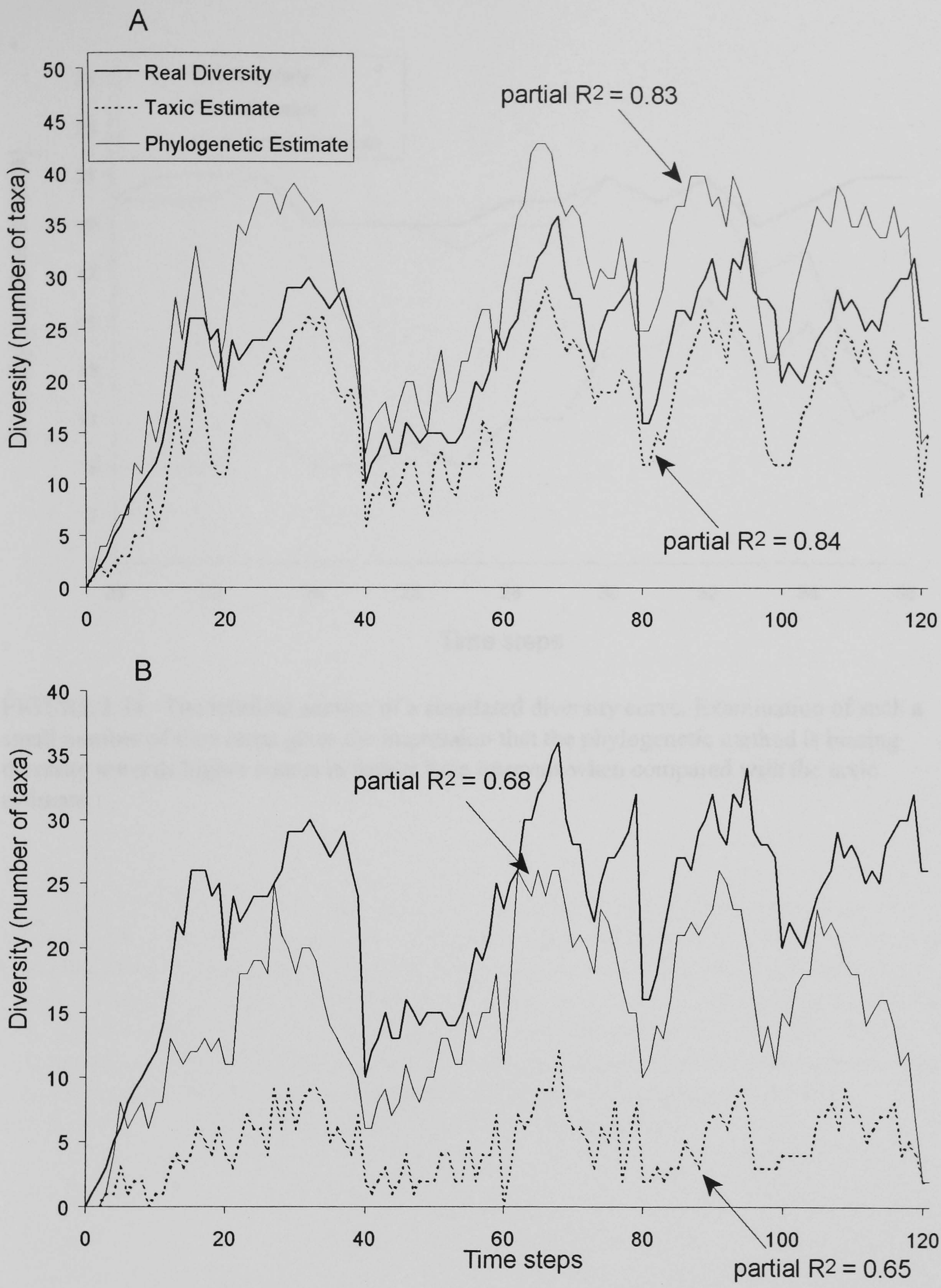


FIGURE 2.23. The efffect of sampling intensity on diversity patterns. (A) Sampling rate = 0.5 (B) Sampling rate = 0.1. The lower sampling intensity magnifies the Signor-Lipps effect seen in the phylogenetic estimate prior to mass extinction events and at the termination of the diversity history of a clade.

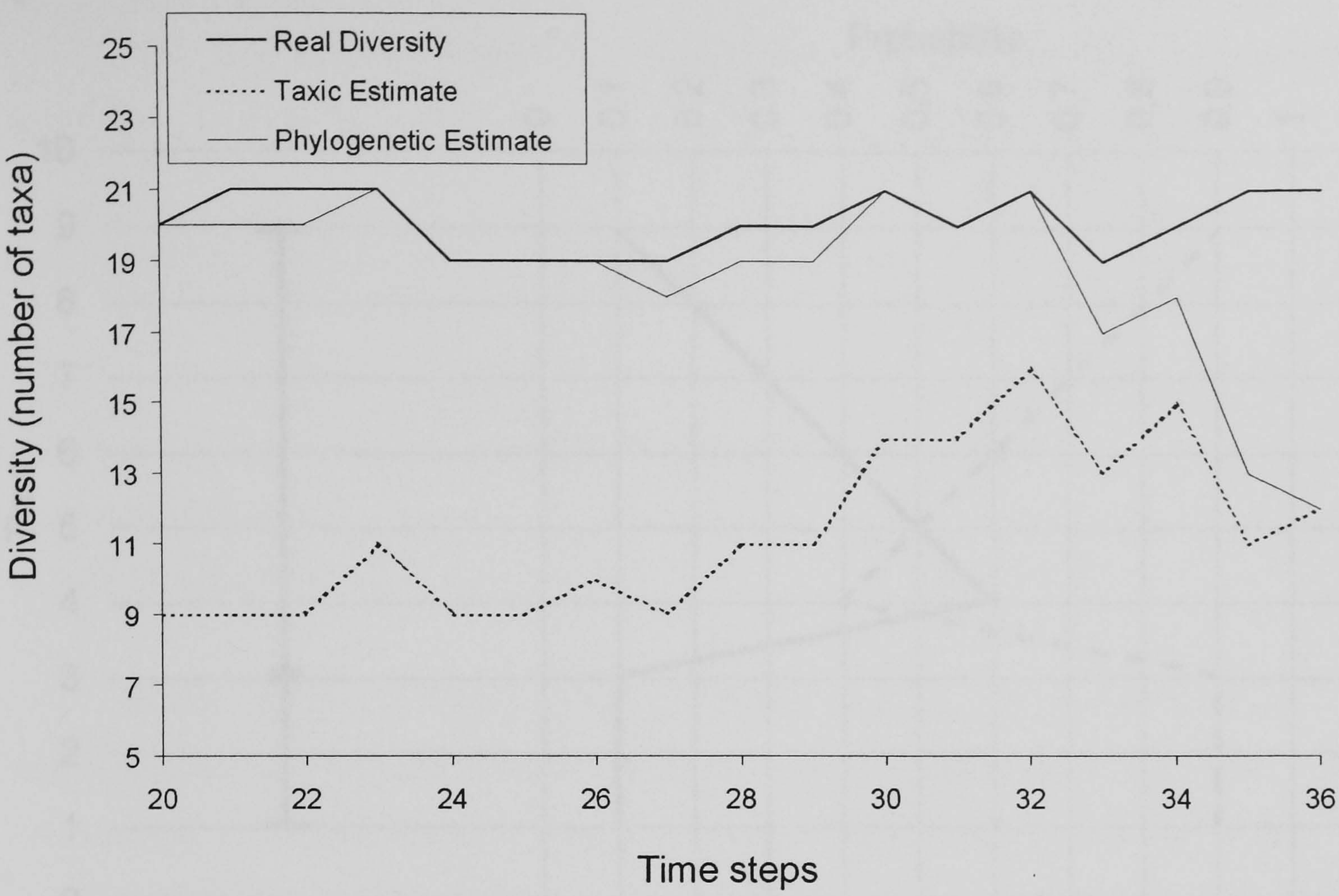


FIGURE 2.24. The terminal section of a simulated diversity curve. Examination of such a small number of time steps gives the impression that the phylogenetic method is biasing diversity towards higher counts in earlier time intervals when compared with the taxic estimate.

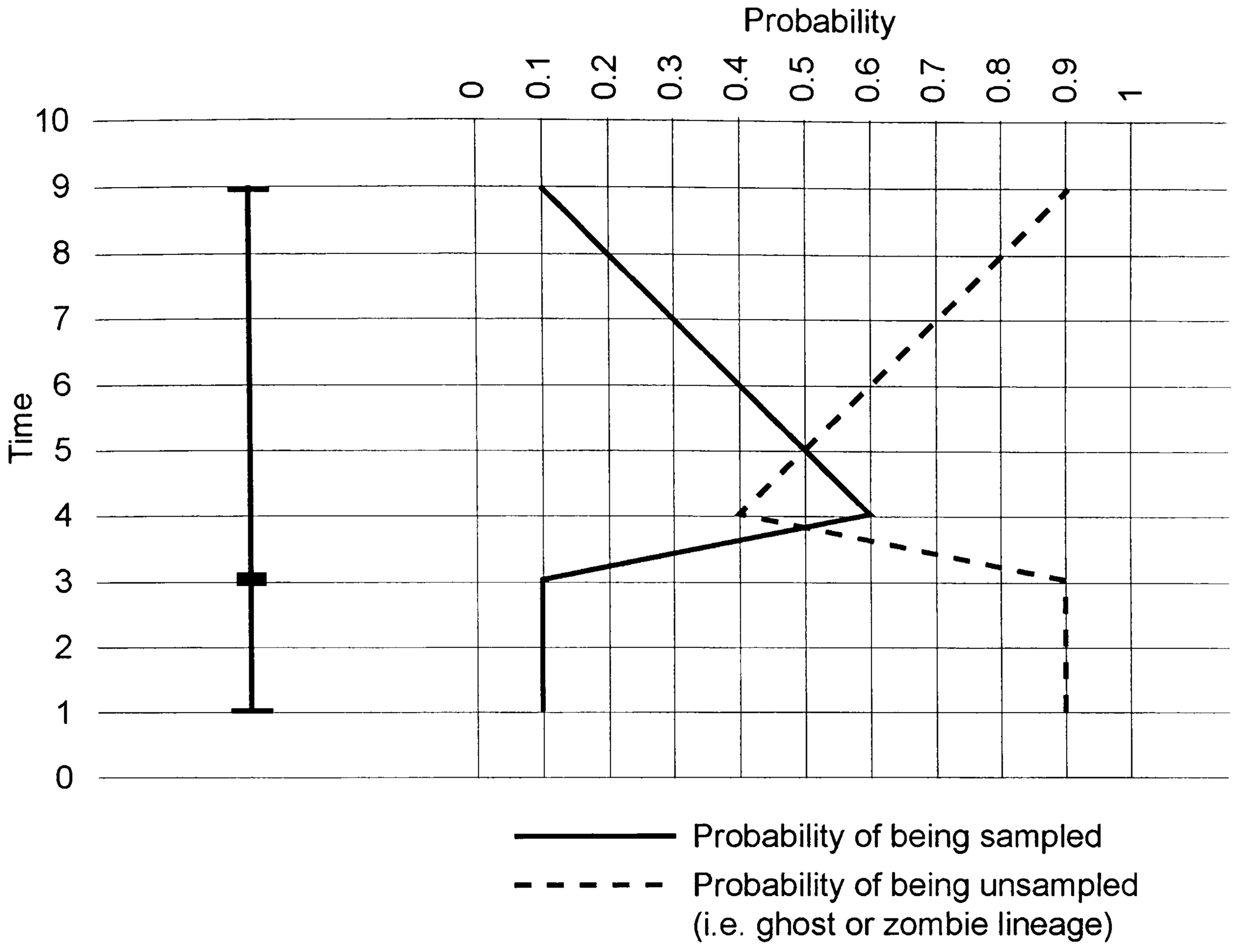


FIGURE 2.25. The relationship between range length and sampling probability. A taxon originates at time 1, under conditions of a uniform sampling probability of 0.1 occurences per time step. Until its first appearance in the fossil record it has a probability of 0.1 of being sampled in each time interval. However, after its first appearance the sampling probability in each time interval becomes 0.1 + (number of time intervals until extinction x 0.1). This is because a fossil appearance later in the taxon's lifespan will fill in all the intermediate range. As a consequence the probability of a taxon's range being unsampled after its first appearance, i.e.. zombie lineage, increases with time to extinction.

After the first sampled interval the probability of any one interval being recorded in the final recorded range is:

$$p_{\text{range}} = r_{sam} + (t \times r_{sam}) \qquad \text{(eq. 2.2)}$$

where:

p_{range} = probability of the time interval being recorded in final range

r_{sam} = sampling rate

t = time to extinction

Hence, once a taxon had been sampled for the first time, the probability of any one subsequent interval being sampled decreases with decreasing time to extinction. During most of the diversification history of a clade these decreasing probabilities are evenly distributed through time as taxa originate and go extinct randomly. However at coordinated extinction times, such as mass extinctions, many taxa reach the end of their range simultaneously, and the result is an overall reduction in sampling probabilities. This is the sampling artefact that can make a catastrophic mass extinction look like a gradual one (Fig 2.26) and it was first out-lined by Signor and Lipps (1982).

An important consequence of the Signor-Lipps effect is that not only does the proportion of unsampled relative to sampled range increase, but also this unsampled range is at the terminal end of the life span of taxa. Therefore the ratio of zombie lineages compared to ghost lineages rises during these periods, and also the ratio of *terminal taxa* zombie lineages as compared to *ancestral taxa* zombie lineages rises. Hence this is the reason why the phylogenetic method produces a skewed diversity pattern in the time intervals leading up to bursts of taxonomic last-appearances, but not in other periods of a clade's history. It is also the reason why this skew is not so apparent if ancestors are not sampled. The Signor-Lipps effect is also evident in the taxic estimate, but due to the inability of the phylogenetic estimate to correct for late unsampled range, the effect is *exaggerated* by the use of this method.

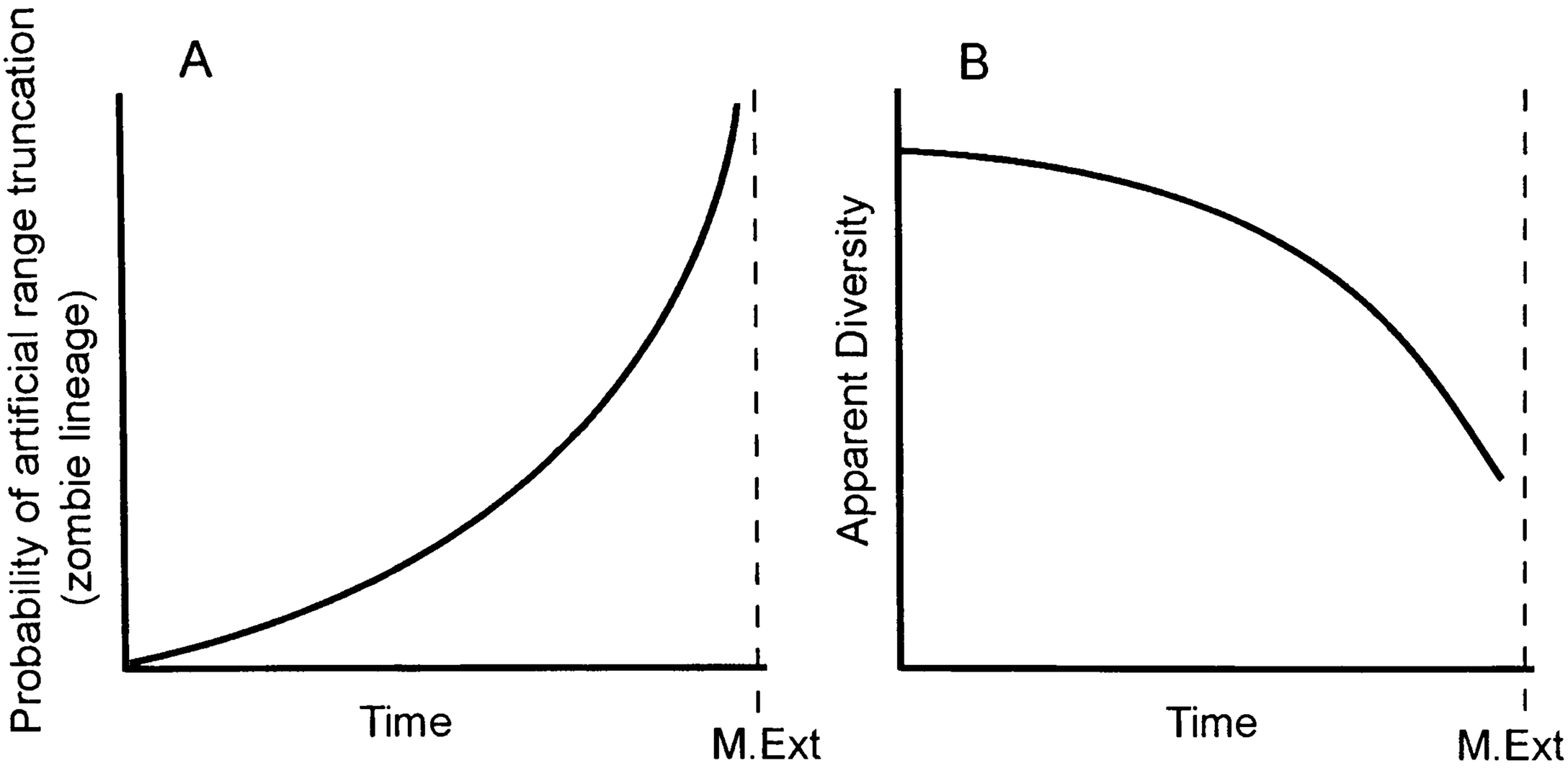


FIGURE 2.26. The Signor-Lipps effect. The probability of a taxon being resampled after its first appearance in the fossil record decreases with decreasing time to extinction, as shown in Fig. 2.17. (A) As a consequence if there is a coordinated burst of extinctions, e.g. a mass extinction event, the amount of artificial range truncation (Signor and Lipps 1982), or zombie lineage, increases with decreasing time to the event. (B) This is will have the effect of making a catastrophic mass extinction look gradual (after Signor and Lipps1982, Fig. 2).

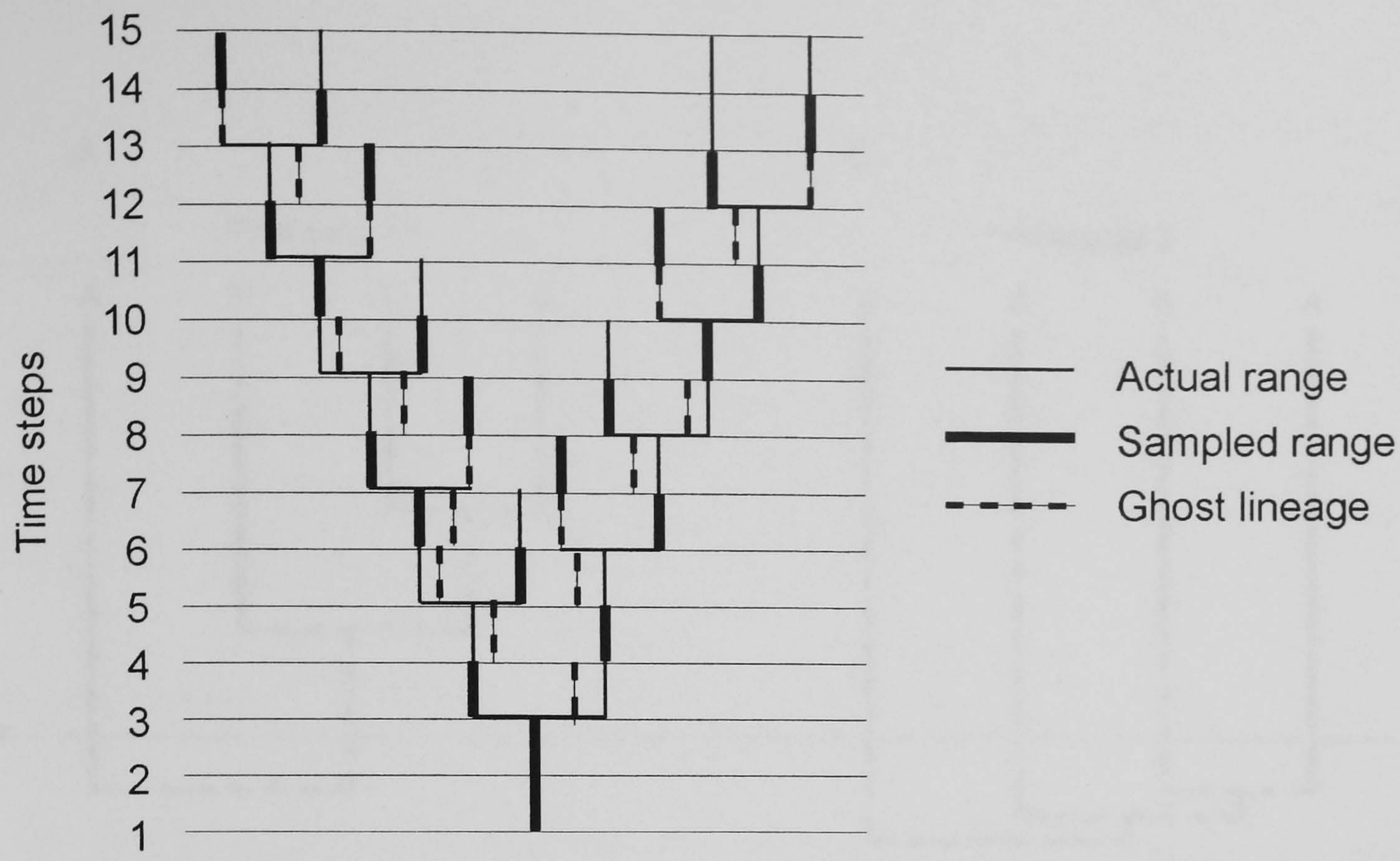
The problem of ancestors

Dealing with suspected ancestors using the phylogenetic method is difficult. Norell (1993) assumed that no ancestors were present in his theoretical examples. He described ghost taxa as 'the kinds of ghost lineage that are embedded in the internal structure of trees… These taxa become extinct by speciating into terminal taxa' (Norell 1993, pp 411), in other words ancestral taxa that have not been recovered from the fossil record. Smith (1994), however, acknowledged that ancestral 'metataxa' (Archibald 1994) may be discovered in the fossil record and included in cladograms and evolutionary trees. The results of the GHOSTRANGE_A program runs performed here demonstrate that the inclusion of ancestral taxa in phylogenies that are erroneously diagnosed as sister taxa to their descendent groups will inflate the diversity counts produced using the phylogenetic method. This problem is eliminated in the diversity curves produced by the GHOSTRANGE_B version of the program, hence Smith's (1994) suggestion that ghost ranges should only extend from the first appearance of a descendent group down to the *last* appearance of a putative ancestor is required if the phylogenetic method is to correctly reproduce the diversity magnitude of a clade. A theoretical clade sampled uniformly, and with ghost lineages added correctly according to Smith's method, does not show heightened diversity levels (Fig. 2.27), however the artificial diversity decrease at the end of the history of the clade is still evident.

Other problems with the phylogenetic method

The results of this analysis confirm that the phylogenetic method of estimating diversity does improve diversity patterns in the majority of situations for clades of between 100 and 500 taxa. However, many phylogenetic studies are performed on much smaller clades diversifying over few time intervals. It is likely that the diversity distortion of the phylogenetic method prior to clusters of extinctions as identified here will become of greater consequence for smaller-scale studies. In addition, the phylogenetic method can only be used for studies of clades that have a robust cladogram. It is therefore not feasible for large-scale investigations involving many different groups of organisms, such as the analysis of global diversification. Finally, the phylogenetic method is only as reliable as the cladogram upon which it is based. The simulation used here assumes perfect phylogenetic knowledge. However, the use of different cladograms will produce different diversity estimates (Fig. 2.28). The phylogenetic relationships of many groups

A



B

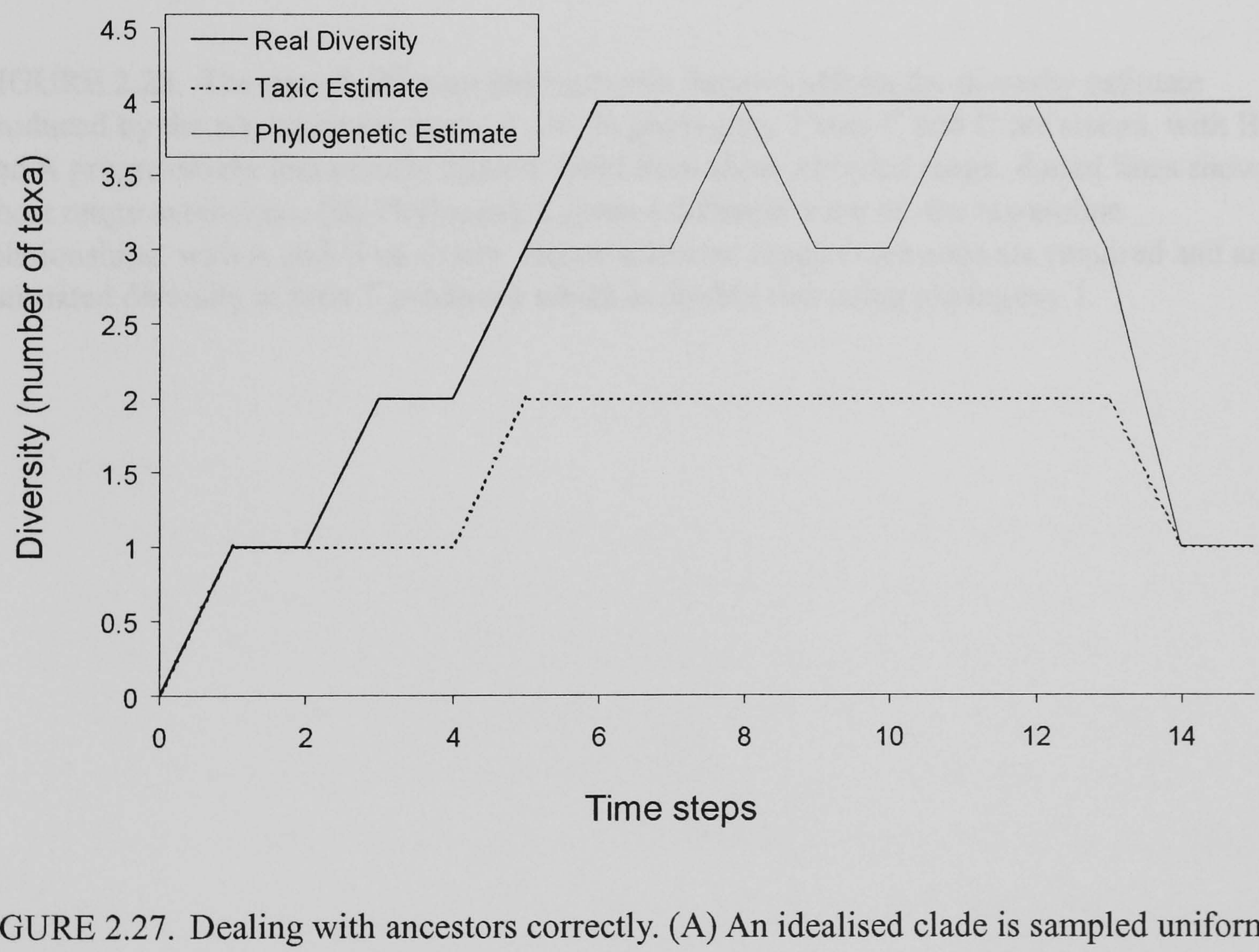


FIGURE 2.27. Dealing with ancestors correctly. (A) An idealised clade is sampled uniformly to produce an even and equal distribution of ghost and zombie lineages. Ghost lineages are only inserted from the first appearance of the descendent group down to the last appearance of the ancestral taxon. (B) The resulting diversity curves demonstrate that the phylogenetic method only over-estimates diversity if ancestors are misdiagnosed. However, the decrease in diversity at the end of the curve is still evident. Even if ancestral taxa are correctly diagnosed, the phylogenetic method still exaggerates the Signor-Lipps effect in the time intervals prior to clusters of extinctions, due to the increased ratio of terminal taxa zombie lineages when compared to ghost lineages, and ancestral taxa zombie lineages.

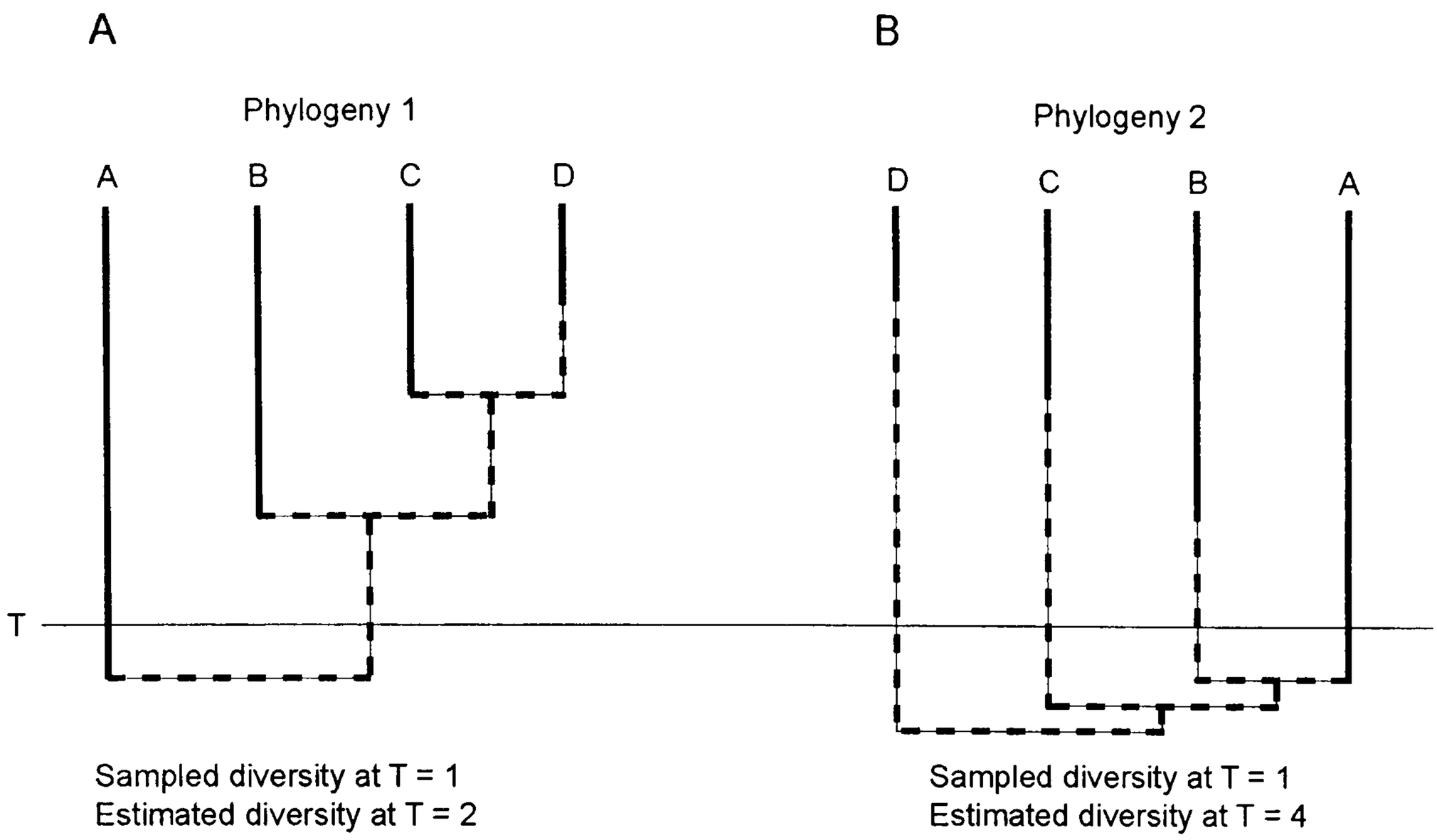


FIGURE 2.28. The use of different phylogenetic theories effects the diversity estimate produced by the phylogenetic method. (A) In phylogeny 1 taxa C and D are sisters, with B and A progressively less closely related. Bold lines show sampled range, dotted lines show ghost range extensions. (B) Phylogeny 2 gives a different view of the taxonomic relationships, with A and B as sisters. Hence different range extensions are required and an estimated diversity at time T produced which is double that using phylogeny 1.

are in constant review, may change with new discoveries, and may be the subject of several conflicting trees. In addition, the accuracy of a phylogenetic reconstruction and the sampling probability of a fossil group are not independent. A poorly sampled group, one containing taxa with substantial range gaps, and many unsampled members, is also likely to have an inaccurate phylogenetic reconstruction (Huelsenbeck 1991; Wagner 2000), hence reducing the reliability of any implied range extensions and diversity estimate enhancements.

2.5. Conclusions

- In the majority of simulations the phylogenetic estimate captured the real pattern of diversity better than the taxic estimate. The performance of the phylogenetic estimate is reduced in studies of small clades whose members are predominantly extinct. Where a clade has an exponential diversification pattern, and few extant representatives or where there is imperfect sampling in the final time interval, the taxic estimate is superior to the phylogenetic.
- In situations where ancestors are sampled and misdiagnosed as sister taxa to their descendents, and where sampling rate is high, the phylogenetic method significantly over-estimates diversity levels. This problem is eliminated if the phylogenetic method is adjusted to correctly insert ghost lineages with respect to ancestors.
- The taxic estimate artificially reduces diversity prior to mass extinction events, and at the end of the history of a clade where there is imperfect sampling in the final time interval, due to the Signor-Lipps sampling effect. The phylogenetic estimate magnifies and extends this decline in diversity. Hence, the phylogenetic estimate yields inaccurate patterns for clades diversifying over few time-steps.
- The phylogenetic estimate is considered appropriate for diversity studies of large clades with many extant representatives, and where any fossil taxa are reasonably well sampled. A poorly sampled group will reduce the accuracy of the phylogenetic reconstruction and hence the reliability of range extensions.
- If a clade includes many putative ancestral lineages, and where the study is predominantly of extinct taxa, and contains large extinction events, the taxic approach is more appropriate for estimating diversity patterns.

- These results assume accuracy in phylogenetic reconstruction. Errors in phylogeny may strongly reduce the performance of the phylogenetic method in estimating diversity patterns.

CHAPTER 3. THE PALAEOZOIC PLATEAU – AN ARTEFACT OF TAXONOMIC LEVEL?

3.1 Introduction

The strongest evidence for the multiple equilibria model of Phanerozoic biodiversification (Sepkoski 1978, 1979, 1984; see also Courtillot and Gaudemer 1996) is the *shape* of the global marine diversity curve from the Precambrian to the present, in particular the shape of the curve as plotted at the taxonomic level of the family. In his first paper on the subject Sepkoski (1978) plotted the marine diversity curve at ordinal level, and identified the explosive origination periods of the Cambrian and Ordovician followed by a single equilibrium running through to the Recent, punctuated by perturbations, i.e. periods of higher than average numbers of extinctions and originations. It was on this basis that the logistic model of biodiversification was proposed, with the term *kinetic model* used to highlight the dynamic nature of the equilibrium. The use of taxonomic orders in this study was defended by Sepkoski thus: "As large entities, orders tend to smooth out, much like running averages, many minor fluctuations in diversity, thus making the fundamental patterns more readily discernible" (Sepkoski 1978, p. 224). However it is at familial level that the multiple equilibria model is revealed fully (Sepkoski 1979), and in this study families were considered to provide data superior to orders. Due to "greater numbers and shorter average durations, families are capable of revealing subtle, short-term patterns and trends in diversity that are not clearly visible with higher taxa" (Sepkoski 1979, p. 225).

This switch from orders to families illustrates the problems associated with choosing the taxonomic level at which to conduct a biodiversity study: higher taxa are less affected by the vagaries of sampling in the fossil record and are thought to provide more robust diversity patterns, but by their long-term nature they may mask much of the shorter term or more subtle patterns. Although much of the decision lies upon the scale of the biodiversity pattern under investigation, orders are generally thought too coarse for use even in long-term global studies. Bambach (1989) predicted that genera and families, constructed as assemblages of species with similar morphologies, are useful for diversity studies, while orders, classes and phyla are defined by key characters and therefore will exhibit diversity histories decoupled from those of species. The majority

of recent global palaeodiversity analysis has been conducted at the level of the family or genus.

Is the use of taxa ranked higher than species legitimate? It can be argued that genera and families are biological entities in their own right, in the same way as species, and therefore valid as units of diversity. Each consists of a set of species specialised for a particular mode of life or niche. If this set of niches as a group represents some ecological sub-division, then the higher taxon can be seen as a biological entity occupying that sub-division. Some workers embrace this interpretation (e.g. Simpson 1961; Bottjer and Jablonski 1988; Valentine 1990; Van Valen 1984, 2002 pers. comm.) arguing that both monophyletic and paraphyletic higher taxa are biologically meaningful entities.

In general, however, when higher taxa are used in biodiversity studies it is as proxies for species, hence it is the pattern of species diversification through time that we are attempting to discover (Sepkoski 1978). Unfortunately, species data are only available for the most localised of biodiversity analyses. The large number of fossil species described means that there is little immediate hope of any individual or research group compiling a global species-level taxonomic database. Paradoxically the most fundamental problem in the use of fossil species is the incompleteness of their record. Raup (1995) estimated that only one per cent of all the species that have ever existed has been preserved, discovered and described. However, as only one species is required to establish the presence of a genus, and only one genus to establish the presence of a family, the fossil record is assumed to become increasingly more complete at higher taxonomic ranks. Finally, species suffer more from the subjective nature of taxonomic practice than either genera or families (Kemp 1999); therefore the use of species in diversity studies may produce spurious and inaccurate results.

Hence plotting global diversity curves at the level of genera, families or even orders is currently necessary. How confident can we be that the patterns of diversification uncovered at higher taxonomic levels accurately reflect the true pattern of species diversity? If the distribution of species among the higher taxa is uneven, it is unlikely that a plot at familial level will accurately match the species-level pattern. Computer simulations (Sepkoski 1978; Sepkoski and Kendrick 1993) have predicted an adequate association between diversity counts at differing taxonomic levels, while a study comparing diversity patterns of extant eastern Pacific molluscs at the level of genus and family to that at species level found a good correlation (Roy et al. 1996). The

fossil evidence, however, is equivocal. Sepkoski (1997) claimed a strong overall similarity between the global diversity histories of fossil marine families and genera, although he noted differences in the detail of the curves. McCormick and Owen (2001) noted good correlations between the diversity curves of Ordovician trilobite genera and species from the Welsh Basin. Conversely Signor (1985) showed a poor match between estimated numbers of fossil species and empirical counts of higher taxa. A recent study of species richness and higher taxon diversity in both living and fossil plant communities (Enquist et al. 2002) found that although there was a tight relationship between the number of species, and the number of genera and families within the samples, this relationship was not one-to-one, but a power-function. As species richness increased, so generic and familial diversity increased but at a slower rate. Knowledge of the slope of this function for any particular type of habitat or community would be required before any prediction of species richness could be made from the diversity of higher taxa. There is also the question of timing in the origins of species and higher taxa. Raup (1983) observed that higher taxa should be expected to appear early in the fossil record, while lesser ranked taxa, genera and species, can appear at any point throughout the group's history. As a consequence, standing diversity at higher taxonomic levels tends to be stable or to decline through time following the initial radiation. This pattern may be totally decoupled from that at species level, which may require a different model of diversification than those derived from data at higher taxonomic ranks (Kitchell and Carr 1985) .

As a result of these problems the appropriateness of families as the units of taxon counting has been questioned. Using various palaeontological sampling measures to model species richness, Signor (1985) suggested that higher taxa are not good indicators of species diversity. Flessa and Jablonski (1985) noted the regular increase in the number of species per family since the Silurian, and concluded that it is this taxonomic distribution, rather than any ecological controls, that causes the decline in family extinction rates though the Phanerozoic. Similarly Benton (1995, 1997, 2001) proposed that the multiple equilibria pattern of marine diversification seen in the fossil record is an artefact of the taxonomic level at which the data have been plotted, and predicted that the equilibria seen at familial level, in particular the Palaeozoic diversity plateau, will break down at the lower taxonomic levels of genera and species. On publication of his marine generic global Phanerozoic diversity curve, Sepkoski acknowledged that "the greater sensitivity of genera to perturbations detracts from a

strong appearance of equilibrium through the middle to late Paleozoic Era" (Sepkoski 1997, p. 535).

While it is still not possible to do more than model diversity at species level on a global scale, there are now several large datasets containing fossil taxonomic range information, the manipulation of which allows diversity curves to be plotted and compared for many different taxonomic and ecologic groups, at various taxonomic levels and over differing time scales. In this way we can aim to understand the relationship between taxonomic level and the perceived diversity pattern of any particular group.

3.2. Analysis methods

3.2.1. Use of global taxonomic databases

The use of large, computer-held collections of fossil taxonomic occurrence data has become standard in the study of palaeobiodiversity dynamics (see Benton 1999 for review), whether the focus is taxonomic radiation periods (e.g. Miller and Foote 1996; McCormick and Owen 2001), extinction events (e.g. Raup and Sepkoski 1982, 1984; Sepkoski 1996b; Courtillot and Gaudemer 1996) or long-term trends within diversity patterns (e.g. Sepkoski 1978, 1979, 1981, 1984; Benton 1995, 1997). Two published compendia, one of marine fossil animal families (Sepkoski 1992) and the other consisting of fossil animal and plant families from all habitats (Benton 1993) are widely used, Sepkoski's marine genera database (see Sepkoski 1996b for description) has been used in recent publications (e.g. Sepkoski 1997; Adrain and Westrop 2000; Foote 2000a, b, 2001). Such data collections consist of first and last appearance dates for fossil taxa. From this information, taxonomic time ranges can be calculated, and hence standing diversity through time, and turnover rates. In recent years the ease of manipulation of such large datasets has been facilitated by the increasing power and availability of computers and software such as relational database management systems. The data, however, continue to suffer from the problems of poor taxonomy, uneven stratigraphic resolution and variations in sampling intensity (Johnson and McCormick 1999), requiring caution to be exercised when interpreting any results. The compendia also draw upon similar sources of information, e.g. the *Treatise on Invertebrate Paleontology* (Moore et al. 1953-2000), and therefore are not wholly independent. A

new *sampling standardised* database currently under construction aims to go some way towards correcting these errors, in particular those of sampling intensity (Alroy 2000; Alroy et al. 2001). The time required for this resource to reach the level of coverage of the Sepkoski and Benton datasets is still undetermined. Until then the use of the currently available global first and last appearance taxonomic datasets remains the best way of uncovering the patterns of global biodiversity dynamics.

3.2.2. The TAXONOMIC database

To investigate the nature of Phanerozoic diversity curves a new relational database named TAXONOMIC has been created to hold several large taxonomic datasets alongside stratigraphic information. TAXONOMIC has been created using the Microsoft Access RDBMS (relational database management system). The Access program allows the creation of many interrelated tables of data. It also allows *queries* to be created and executed using Structured Query Language (SQL).

The data tables within the TAXONOMIC database can be divided into two types: those holding taxonomic information and those holding stratigraphic information (Fig. 3.1). Taxonomic tables were originally designed to hold data from the *Fossil Record 2* dataset (Benton 1993). Further tables have been added as other datasets have become available: Sepkoski's compendium of fossil marine animal families (Sepkoski 1992) and Sepkoski's unpublished dataset of fossil marine genera (see Sepkoski 1996b for description).

Stratigraphic tables hold geological interval names and codes as used by the taxonomic datasets, along with chronological information.

The TAXONOMIC database can be found on the IBM disc accompanying this thesis (See Appendix II for description of IBM disc contents). Only the family data tables and SQL queries are included, the genus data and associated SQL queries have been removed from the TAXONOMIC database as permission has not been granted to distribute this unpublished data.

The following is a brief description of the main tables within the TAXONOMIC database. All are referenced in Figure 3.1.

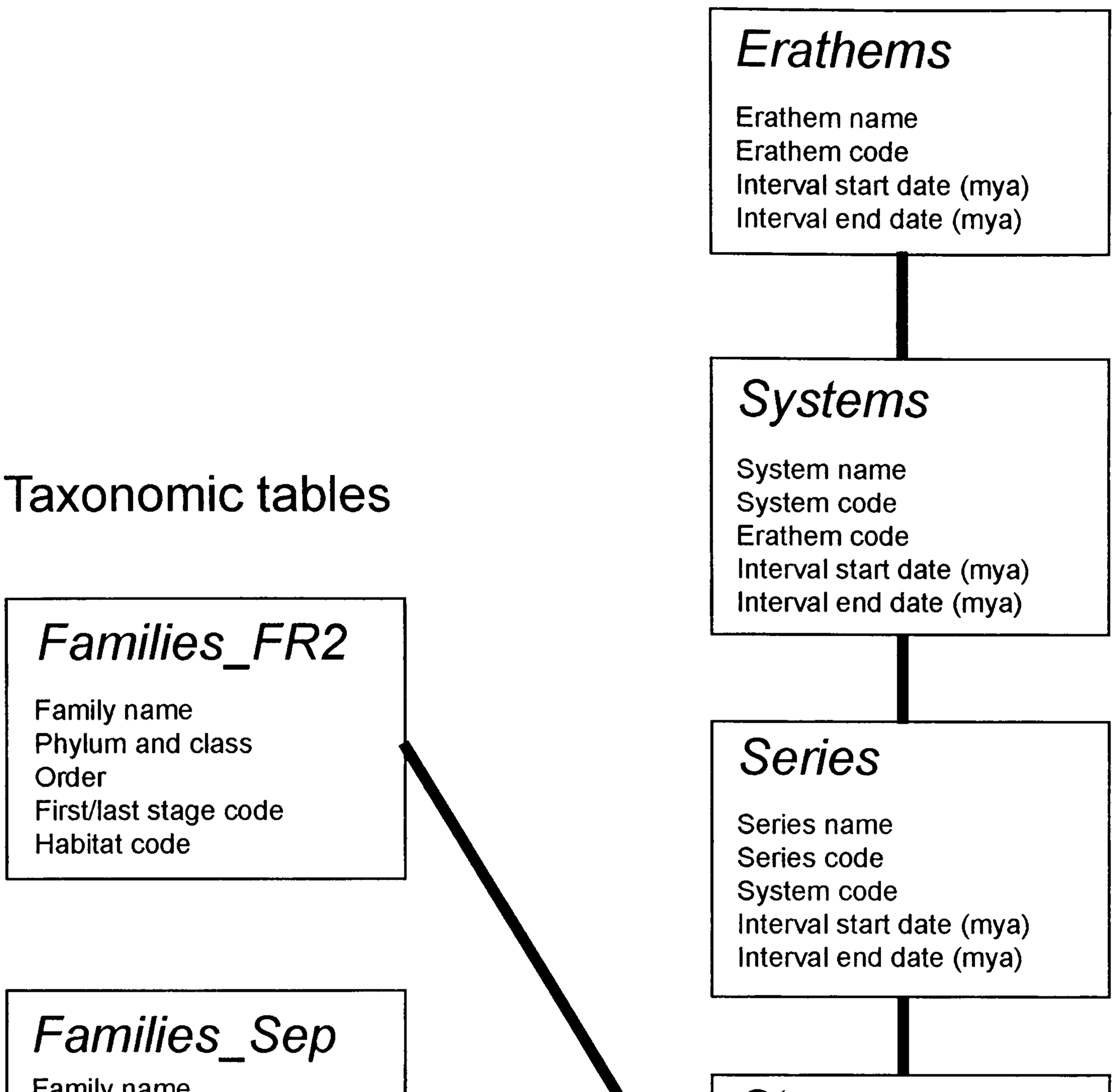


FIGURE 3.1. Structure of the TAXONOMIC database. Boxes represent tables within the database. Each table name is shown in italicised text, followed by descriptions of the primary fields contained within. Bold lines represent relational links between the tables.

3.2.2.1. Taxonomic data tables

Families_FR2

The data within this table is the complete *Fossil Record 2* dataset (see Benton 1993 for description) which is available for download from the internet at: http://palaeo.gly.bris.ac.uk/frwhole/FR2.html. This dataset contains the fossil ranges of all known families of terrestrial and marine plants and animals (6539 records), with the majority of first and last appearances resolved to the level of stratigraphic stage as set out in Harland et al. (1990). The exceptions are Palaeozoic (apart from Devonian) appearances which are resolved to the level of series according to Harland (although see the Geological Society of America's 1999 time scale http://rock.geosociety.org/science/timescale/timescl.pdf where these divisions are given as stages). Each family record consists of the following information:

- Family name
- Higher taxon names (phylum and class)
- Order name (only included for the ten dominant classes of the Palaeozoic fauna)
- Stage code of first and last appearances, both certain and uncertain
- Habitat code (T = Terrestrial, M = Marine, F = Freshwater, B = Brackish water, L = Lagoonal, V = Volant, S = Littoral).

Table 3.1 illustrates a section of this data table showing column headings and an example of the *Fossil Record 2* data contained within.

Families_Sep

This table holds Sepkoski's compendium of fossil marine animal families (Sepkoski 1992 with updates, 4076 records). First and last appearances are resolved to the level of the stage intervals given in Sepkoski (1992). A number of families (36%) have first and last appearances resolved to substage level. Each family record consists of:

- Family name
- Higher taxon names (phylum, class)
- Order name
- System code of first and last appearance
- Stage code of first and last appearance

Family_name	Higher_taxon_names	Order_name	First_stage_certain	Last_stage_certain	First_stage_uncertain	Last_stage_uncertain	Habitat_code
Abadehellidae	Protozoa				UFI	TAT	M
Abadiellidae	Arthropoda.Trilobita		CRF_SR	CRF_SR			M
Abelisauridae	Chordata.Reptilia		CEN	MAA	ALB		T
Abrocomidae	Chordata.Mammalia		UMI_SR	REC			T
Abrograptidae	Graptolithina		ARG_SR	CRD_SR			M
Acadiocarididae	Arthropoda.Malacostraca				TOU_SR	SPK_SR	M
Acanthastrellidae	Porifera.Demospongia		KIM	CMP	OXF		M
Acanthisittidae	Chordata.Aves		HOL	HOL			T
Acanthoceratidae	Mollusca.Cephalopoda	Ammonoidea	CEN	CON			M
Acanthochaetetidae	Porifera.Demospongiae		APT	REC			M
Acanthochitonidae	Mollusca.misc		CHT	REC			M
Acanthocladiidae	Bryozoa.Stenolaemata	Fenestrata	LUD_SR	TAT	WEN_SR		M
Acanthocnemidae	Arthropoda.Insecta		TOA	REC	HET		T
Acanthodesmiidae	Protozoa				DAN	HOL	M
Acanthodidae	Chordata.Acanthodii		FRS	SAK			MF
Acanthodontidae	Chordata.Conodonta		TRE_SR	LLN_SR			M
Acanthogammaridae	Arthropoda.Malacostraca		UMI_SR	REC			F
Acanthograptidae	Graptolithina		MER_SR	LOK			M
Acanthonematidae	Mollusca.Gastropoda	Archaeogastropoda	EIF	ANS		LAD	M
Acanthosomatidae	Arthropoda.Insecta		MMI_SR	REC			T
Acanthostegidae	Chordata.Amphibia		FAM	FAM			F
Acanthotelsonidae	Arthropoda.Malacostraca		SPK_SR	ASS		KUN	F
Acanthuridae	Chordata.Osteichthyes		LUT	REC			M
Acaridae	Arthropoda.Chelicerata		RUP	REC			T
Acaroceratidae	Mollusca.Cephalopoda	Ellesmerocerida	MER_SR	MER_SR			M

Table 3.1. Example section of the *Families_FR2* table of the TAXONOMIC database. The field headings are typical of all the data tables containing taxonomic information. Stage codes are those used in the *Fossil Record 2* (Benton 1993) data set, with the suffix '_SR' used to denote a stratigraphic interval listed as a series rather than a stage in Harland et al. (1990). For habitat codes see text.

- Substage code of first and last appearance (if any of these stratigraphic codes do not change from one stratigraphic level to the next this indicates that the taxon's range has not been resolved to the lower stratigraphic level).
- An indication , where appropriate, that the first (F_Unc) or last (L_Unc) appearances are considered uncertain.

Genera

Sepkoski's unpublished compendium of fossil marine genera is contained within this table (36323 records). As with Sepkoski's family compendium the first and last appearances of the majority of genera are resolved to stage level, with some (38%) resolved to substage level. Each genus record contains the same information as that of Sepkoski's family dataset (see above), substituting 'genus name' for 'family name'.

The generic dataset has been slightly modified to take account of the changes in stratigraphic conventions adopted by Sepkoski between the creation of his familial and generic compendia. For example, the Rhaetian stratigraphic division used within the generic dataset is incorporated into the Norian in the familial dataset, and the Siegenian stage of the familial dataset is renamed the Pragian in the generic. These modifications allowed a single stage codes table to be related to both the *Families_Sep* and *Genera* tables.

Despite the general misgivings about the completeness of the fossil record at low taxonomic levels, this database has now been used several times in biodiversity studies (Sepkoski 1996b, 1997; Kirchner and Weil 2000a, b; Foote 2000a, b, 2001) and although certainly incomplete and with many errors, has been demonstrated not to suffer from any statistically systematic bias (Adrain and Westrop 2000).

3.2.2.2. Stratigraphic data tables

Stages – Series – Systems – Erathems

This sequence of related tables contains the stratigraphic interval codes as used within the *Fossil Record 2* (Benton 1993) dataset. Each record within these tables contains:

- Interval name
- Interval code
- Code of next most inclusive interval

- Start and end time in units of millions of years before present.

In addition the *Stages* table contains a stage midpoint date for each interval. This allows diversity data to be plotted at the midpoint of each stage. A suffix of '_SR' after the stage code indicates that the interval is considered a series by Harland et al. (1990). Table 3.2 illustrates a section of the *Stages* data table showing column headings and an example of the stratigraphic data contained within.

The *Fossil Record 2* uses a total of 77 Phanerozoic stratigraphic intervals with a mean interval duration of 7.05 million years and a standard deviation of 4.52 million years.

Stages_Sep

This second stage table was required as the Sepkoski compendia do not use the same stratigraphic scheme or interval codes as the *Fossil Record 2*. Each stage record within the table contains:

- Stage code
- Start and end time (millions of years before present)
- Stage midpoint (millions of years before present).

The Sepkoski compendia use a total of 81 Phanerozoic stratigraphic intervals with a mean interval duration of 6.57 million years and a standard deviation of 3.56 million years. The smaller mean and standard deviation are due to the Sepkoski scheme splitting the Cambrian into eleven stages as compared to the three Cambrian series used in the *Fossil Record 2*.

3.2.2.2. Dates of stratigraphic intervals

The dates of Harland et al. (1990) have been updated using the Geological Society of America (GSA) 1999 Geologic Time Scale (http://rock.geosociety.org/science/timescale/timescl.pdf). The Cambrian interval dates pose a particular problem. The date of the Cambrian base has recently been moved (Landing 1994) and stage dates are in a state of investigation by the International Subcommission on Cambrian Stratigraphy (ISCS), a division of the International Union

Stage name	Stage id	Series id	Start time	End time	Stage_midpoint
Holocene	HOL	HOL	0.01	0	0.005
Pleistocene	PLE	PLE	1.8	0.01	0.905
Pliocene	PLI_SR	PLI	5.3	1.8	3.55
Upper Miocene	UMI_SR	UMI	11.2	5.3	8.25
Middle Miocene	MMI_SR	MMI	16.4	11.2	13.8
Lower Miocene	LMI_SR	LMI	23.8	16.4	20.1
Chattian	CHT	OLI	28.5	23.8	26.15
Rupelian	RUP	OLI	33.7	28.5	31.1
Priabonian	PRB	EOC	37	33.7	35.35
Bartonian	BRT	EOC	41.3	37	39.15
Lutetian	LUT	EOC	49	41.3	45.15
Ypresian	YPR	EOC	54.8	49	51.9
Thanetian	THA	PAL	61	54.8	57.9
Danian	DAN	PAL	65	61	63
Maastrichtian	MAA	SEN	71.3	65	68.15
Campanian	CMP	SEN	83.5	71.3	77.4
Santonian	SAN	SEN	85.8	83.5	84.65
Coniacian	CON	SEN	89	85.8	87.4
Turonian	TUR	GAL	93.5	89	91.25
Cenomanian	CEN	GAL	99	93.5	96.25
Albian	ALB	GAL	112	99	105.5
Aptian	APT	GAL	121	112	116.5
Barremian	BRM	GAL	127	121	124
Hauterivian	HAU	NEO	132	127	129.5
Valanginian	VLG	NEO	137	132	134.5
Berriasian	BER	NEO	144	137	140.5
Portlandian	POR	MLM	151	144	147.5
Kimmeridgian	KIM	MLM	154	151	152.5
Oxfordian	OXF	MLM	159	154	156.5

Table 3.2. Example section of the *Stages* table of the TAXONOMIC database. The field headings are typical of all the data tables containing stratigraphic information, accepting the 'stage_midpoint' field which is unique to the *Stages* and *Stages_Sep* tables. Stage and series codes are those used in the *Fossil Record 2* (Benton 1993) data set, with the suffix '_SR' after the stage id used to denote a stratigraphic interval listed as a series rather than a stage in Harland et al. (1990). Start, end and midpoint times for stages are in millions of years before present.

of Geological Sciences (IUGS). There is no international agreement on the number or boundaries of chronostratigraphic divisions of the Cambrian (Davidek et al. 1998). Cambrian subdivision names given in the GSA time scale have been taken from the newly proposed nomenclature for the Cambrian of Laurentia (Palmer 1998). These are not yet applicable globally and they do not correspond to the British series names given in the *Fossil Record 2* (Benton 1993), or to the stage names used by Sepkoski (Sepkoski 1979, 1992).

Therefore dating the Cambrian subdivisions has been achieved using the latest published information from the ISCS with a certain necessary amount of approximation and cross-correlation between the differing subdivision names (Fig. 3.2). The date of the Cambrian base is taken from Bowring et al. (1993), and series boundaries from Davidek et al. (1998). Lower Cambrian stage dates are taken from the estimates of Brasier and Sukhov (1998), which in turn are based upon the radiometric dates of Bowring et al. (1993) and Landing et al. (1998). The Lower Middle Cambrian stages of the Sepkoski scheme (lmid, mMid) approximately correspond to the Amigan stage of Siberia, and the Upper Middle Cambrian stage (uMid) to the Mayan stage of Siberia. This is inferred from Sepkoski (1992) where the Lenian (Toyonian) stage of Sepkoski (1979) has been moved from the Middle to the Lower Cambrian. Dating of the Amigan-Mayan boundary is again taken from Brasier and Sukov (1998), based on an estimate by Shergold (1995), and the boundary of the Sepkoski scheme lMid and mMid Stages has been calculated assuming that they are of the same length (cf. Sepkoski 1979). Dating of the Cambrian-Ordovician boundary is from Davidek et al. (1998). Dates of the three Upper Cambrian stages used in the Sepkoski compendia are problematic as none of the recent publications of the ISCS deals with these divisions. Sepkoski (1979) has the upper Cambrian covering 16 myr, but the new ISCS dates indicate that the Upper Cambrian has a time range of ca 9 myr (Davidek et al. 1998). Therefore the North American Stages used (Dresbachian, Franconian and Trempealeauan) have been scaled down in length to fit the new timescale of the Upper Cambrian. All these inferred dates are approximate.

The Nemakit-Daldyn stage of Sepkoski has been included in the Cambrian and not the Vendian (cf. Rowland et al. 1998; Brasier et al. 1998).

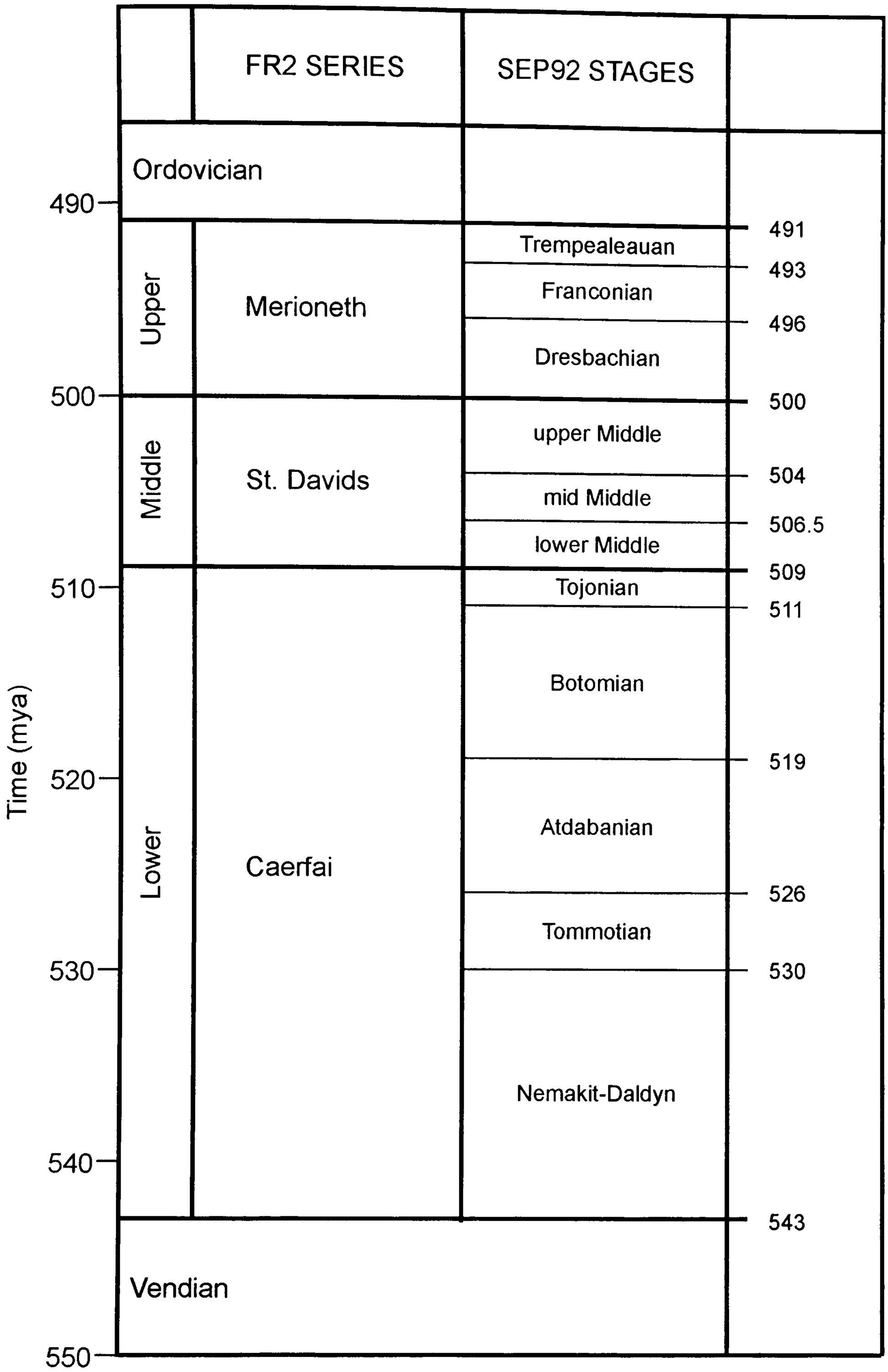


FIGURE 3.2. Cambrian chronostratigraphic chart showing series and stage names used in the *Fossil Record 2* and Sepkoski (1992) data sets. Dates of boundaries shown are those used in the TAXONOMIC database and are adapted from Sepkoski (1979), Bowring (1993), Shergold (1995), Brasier and Sukov (1998), Davidek et al. (1998) and Landing et al. (1998).

3.2.2.4. SQL queries

Structured Query Language (SQL) is a language that allows a database user to communicate with database software, in order to retrieve and modify subsets of data conforming to complicated selection criteria. A piece of SQL code which performs such a task is called a *query*. The Access RDBMS not only allows queries to be run on primary data tables, but also to be run on the results of other queries. Hence a hierarchy of queries can be constructed, each performing a task of retrieving and modifying data, which allows for very complicated data manipulation. Only one operation need be performed to achieve complex data retrieval, matching, modification, grouping, ordering and display.

The following is a brief description of the main queries written for use with the TAXONOMIC database.

DataGroupSelect

This is the primary query upon which the majority of the others are built. When executed it retrieves a subset of data from one of the three taxonomic data tables. The code of the query is modified upon each performance according to the selection criteria required. For example, the following piece of code will retrieve from the *Fossil Record 2* dataset all bivalve and articulate brachiopod families which became extinct at the end of the Permian, excluding singletons, and displays their names, phyla and classes, and stratigraphic ranges (certain occurrences only), ordered alphabetically:

```
SELECT family_name, higher_taxon_names, first_stage_certain,
last_stage_certain
FROM families_fr2
WHERE (higher_taxon_names = 'mollusca.bivalvia' OR higher_taxon_names
= 'brachiopoda.articulata') AND
first_stage_certain<>last_stage_certain AND last_stage_certain = 'TAT'
ORDER BY family_name;
```

StageDuration

This is a simple query which calculates the length of each stratigraphic interval used within the *Fossil Record 2* scheme, for use in calculating diversity rates.

StageDuration_sep performs the same task for the Sepkoski (1979, 1992) stratigraphic scheme.

AllFamMetrics

This query builds upon *DataGroupSelect*, *StageDuration*, and others that link the primary data with the stratigraphic tables. For each stratigraphic interval the query calculates a variety of diversity values and rates describing the subset of *Fossil Record 2* data retrieved, as well as providing the interval midpoint for data plotting purposes. Results are displayed for certain, uncertain and total occurrences. The following diversity values and rates are calculated for each interval:

- Standing diversity
- Number of originations/extinctions
- Percent originations/extinctions
- Total origination/extinction rate
- Per taxon origination/extinction rate
- Per taxon diversification rate
- Per taxon turnover rate
- Mean taxon longevity.

For descriptions and mathematical definitions of the rates see Chapter 1, Section 1.2.1. The two queries *AllFamMetrics_sep* and *AllGenMetrics* perform the same function for subsets of the Sepkoski family and genus compendia respectively.

Per-capita_FR2

This query returns the boundary crosser origination and extinction ratios necessary for calculation of Foote's (2000a) per-capita rates of origination and extinction, for families from the *Fossil Record 2* dataset (see Chapter 1, Section 1.2.1 for description and mathematical definition of these rates). *Per-capita_Sep* and *Per-capita_gen* return the same information for the Sepkoski compendia.

OrdStageDiversityTotal

This query takes the subset of data retrieved by *DataGroupSelect* and calculates standing diversity at order level. For *Fossil Record 2* data this can only be performed

on those families that have ordinal level information (the ten dominant Palaeozoic classes). A similar query *OrdStageDiversity_sep* calculates ordinal level diversity for any subset of the Sepkoski family compendium, as ordinal level information is standard for all families.

3.2.3. Diversity curves and model fitting

The TAXONOMIC database was used to extract diversity counts for each stratigraphic interval through the Phanerozoic for the following groups of animals:

- All life
- Marine life
- Non-marine life
- The three evolutionary faunas (Cambrian, Palaeozoic, Modern) of Sepkoski (1981, 1984; Sepkoski and Miller 1985).

The classes that constitute the three evolutionary faunas have been identified from the factor scores of Sepkoski's (1981) factor analysis. If a class is listed as of importance in more than one fauna, it has been included in the fauna for which it has the highest factor score (cf. Sepkoski 1984), e.g. Bivalvia is included in the Modern fauna despite the fact that it also contributes a significant amount of diversity during the Palaeozoic. Sepkoski's analysis did not yield clearly defined results, and the families within some classes were spread between faunas, attributed to an underlying heterogeneous taxonomic structure (Sepkoski 1984). Therefore only the dominant classes, those constituting 91-93% of each fauna, have been included in the analysis (cf. Kitchell and Carr 1985). Table 3.3 lists the classes assigned to each of the three evolutionary faunas in this analysis.

Cambrian	Palaeozoic	Modern
Trilobita	Articulata	Gastropoda
Polychaeta	Crinoidea	Bivalvia
Monoplacophora:	Ostracoda	Osteichthyes
(Helcionelloida + Tergomya)	Cephalopoda	Malacostraca
Inarticulata (incl. Lingulata)	Anthozoa	Echinoidea
Hyolitha	Stenolaemata	Gymnolaemata
	Stelleroidea:	Demospongia
	(Holothuroidea + Ophiuroidea)	Chondrichthyes
		Hexactinellida

Table 3.3. Marine classes assigned to the three evolutionary faunas.

A published cumulative plot of generic evolutionary faunas (Sepkoski 1997) excludes Recent occurrences of genera with a fossil record, in an attempt to correct for the 'Pull of the Recent' phenomenon (Raup 1979a). This dampens the post-Permian rise in generic diversity. It also reduces the comparability of the generic and family curves because the family curve (Sepkoski 1984, 1997) does not exclude Recent occurrences of families with fossil records. Indeed the 'Pull of the Recent' is likely to be more pronounced in longer-lived taxa such as families (Foote 2000a) rather than genera. Foote (2000a, b) found that excluding from diversity counts Recent genera with a fossil record had a relatively small effect on the results, and concluded that the Cenozoic rise in diversity is unlikely to be entirely an artefact of our extensive knowledge of the Recent fauna. Both plots produced here include Recent occurrences of taxa with fossil records, but exclude extant taxa without fossil records.

The ten classes considered to be the most important during the Palaeozoic in terms of diversity contribution (Sepkoski 1981) have also been plotted. These are the eight classes included in the Palaeozoic fauna in Table 3.3., plus Bivalvia and Gastropoda, which also contribute significantly to Palaeozoic diversity. The two small echinoderm classes Asteroidea and Ophiuroidea have been plotted as one group, equivalent to the 'Stelleroidea' of Sepkoski (1981).

All the diversity plots have been calculated at the greatest number of taxonomic levels (order, family and genus) permissible by the data, and using both the Benton (1993) and Sepkoski (1992, unpub.) compendia. Plots include both total diversity, and diversity minus uncertain families and singletons.

To test the applicability of the exponential and logistic models at the differing taxonomic levels, least-squares fits of each of the relevant equations (Chapter 1, Equation 1.10 and Equation 1.12) were applied to the plots of all life, marine and non-marine life. Models were fit to diversity minus uncertain taxa and singletons data from the final Precambrian interval up until the present. In addition an approximation of the multiple-phase logistic model was applied to the all life and marine data curves by fitting the single logistic equation (Equation 1.12) to the following intervals:

- Cambrian phase
    - *Fossil Record 2* stratigraphic scheme: Vendian – Tremadoc
    - Sepkoski stratigraphic scheme: Vendian – Dresbachian
- Palaeozoic phase

    - *Fossil Record 2* stratigraphic scheme: Tremadoc – Gzelian
    - Sepkoski stratigraphic scheme: Dresbachian – Stephanian
- Meso-Cenozoic phase
    - *Fossil Record 2* stratigraphic scheme: Scythian – Holocene
    - Sepkoski stratigraphic scheme: Induan – Holocene.

For *Fossil Record 2* data curves the first Ordovician stage is included in the Cambrian phase as there are only three Cambrian stratigraphic divisions in this dataset. The Sepkoski scheme, however, has eleven intervals, so the fit is more precise with the latest Cambrian stages excluded from the Cambrian phase (cf. Sepkoski 1984). The Permian is not included in the Palaeozoic phase fit as it is considered to be a 'diversity independent' period outside the scope of the logistic model (Sepkoski 1979). The exponential model has also been fit to the Meso-Cenozoic phase of the all life and marine curves to investigate the possibility that diversification of animal life since the Permian has been exponential rather than logistic.

For each fit the value of the D_0 parameter (initial diversity) was constrained to equal the diversity at the starting point of the curve or phase, or set to 1 if a group's Precambrian diversity was zero – assuming that at least one ancestor was present. The other parameters were calculated according to the best fit of the model to the data. To demonstrate the goodness of fit of the model to the data, R^2 values (coefficient of determination), analysis of variance *F* ratios (ratio of the regression variance to the residual variance), and *p* values (probability that the inferred association between dependent and independent variables based on F is incorrect) were calculated for each regression. An R^2 value tending to 1 indicates a good fit of the model to the data, an *F* ratio increasingly higher than 1 signifies an increasingly stronger association between dependent and independent variables, and a *p* value of <0.05 shows that there is a greater than 95% probability that this association can be relied upon.

The best fit of the logistic model to the three diversity phase sections of the curves was used to determine the two free parameters of the model: the initial diversification rate and the equilibrium level of the system (cf. Sepkoski 1984; Courtillot and Gaudemer 1996). The values of these parameters are a further test of the appropriateness of the model (Courtillot and Gaudemer 1996), in particular the equilibrium parameter (D_{eq}) which can be used to predict future equilibrium levels from the fit of the logistic model to the Meso-Cenozoic data.

3.2.4. Modelling marine diversity at species level

It has been proposed that the apparent logistic pattern of family marine diversity, in particular the Palaeozoic plateau, degrades into an exponential curve at lower taxonomic levels (Benton 1997, 2000). This suggestion was based upon empirical family and genus data, and a model of species diversity produced by Signor (1985) based upon various palaeontological sampling measures. Signor's model was independent of taxonomy. An alternative model is constructed here using the differences in the apparent diversity pattern between the data at family and generic level to infer the pattern at species level. This simple model is based on the assumption that the change in pattern evident between familial and generic data is a real feature of diversity at the differing taxonomic levels and that the change is systematic and of the same form and magnitude as that existing between generic and species level. The percentage differences among the three parameters (D_0, r_0, D_{eq}) of the model fit to the diversity phases at family level, and those at generic level, were calculated. These percentages were then applied to the generic parameters to derive parameters describing the species pattern. A plot of the solutions of the three-phase logistic model using these derived parameters gives a simple approximation of the species-level curve. The familial- and generic-level parameters used to generate the species model are from the curve fitting as applied to the two Sepkoski datasets. The *Fossil Record 2* dataset only has five data points in the Cambrian phase; therefore the logistic fit to this period is unreliable. Also it can be assumed that the two Sepkoski datasets were compiled using similar data collection and recording practices. They also use the same stratigraphic scheme. Therefore the change in diversity pattern from family to genus level is more likely to be a real trend rather than a result of differences in data compilation methods. Random diversity perturbations, in the form of deviations away from the solutions of the derived equations, were applied to the modelled data every ten million years. The incorporation of such stochastic fluctuations into the model produces a more realistic simulation of a natural system (cf. Sepkoski 1978). The magnitude of the deviations was determined by random number generation, within a range of ± 30% of the non-perturbed standing diversity level. This kept the perturbations within the magnitude of the Cretaceous-Tertiary mass extinction event as recorded in the generic data, the largest perturbation in these data after the Permian extinction.

This simple model of species diversity assumes that the taxonomic practices that dictate grouping of genera into families are similar to those governing the grouping of species into genera. Bambach (1989) argued that genera and families will exhibit similar diversity patterns as they are assembled as groups of species with similar morphologies, as opposed to orders, classes and phyla, which are defined by key characters or character complexes. This suggests that the change in diversity pattern from familial level to generic can be applied from genera to species, the unit of each level being merely an increasingly large grouping of the base unit of species. If, however, the degradation in the logistic pattern evident between the familial and generic curves is a feature of poorer sampling at generic level, then the species curve will simply model a similar degradation of sampling between genera and species data, rather than any real diversity signal.

In all the analyses presented here the nature of the Palaeozoic plateau at differing taxonomic levels is investigated in terms of the *shape* of diversity vs. time plots and models. For an investigation of the underlying *rates* of taxonomic turnover, and any effect of taxonomic level on these rates, see Chapter 5.

3.3. Results

3.3.1. Diversity curves – all life, all non-marine, all marine

Phanerozoic global diversity curves for all animal life and all non-marine life plotted at familial level are given in Figure 3.3, and statistics for the model fits are given in Table 3.4.

Group	Data set	Taxonomic level	Time period of fit	Model	R^2	*F*	*p*
All animal life	Benton (1993)	Family	Phanerozoic	Exp.	0.84	404	<0.0001
Non-marine	Benton (1993)	Family	Phanerozoic	Exp.	0.98	3823	<0.0001

Table 3.4. Summary of data, fitted models and fit statistics for Figure 3.3. Exp. = exponential model. R^2 = coefficient of determination, *F* = ratio of regression variance to residual variance, *p* = probability that the association between variables is incorrect.

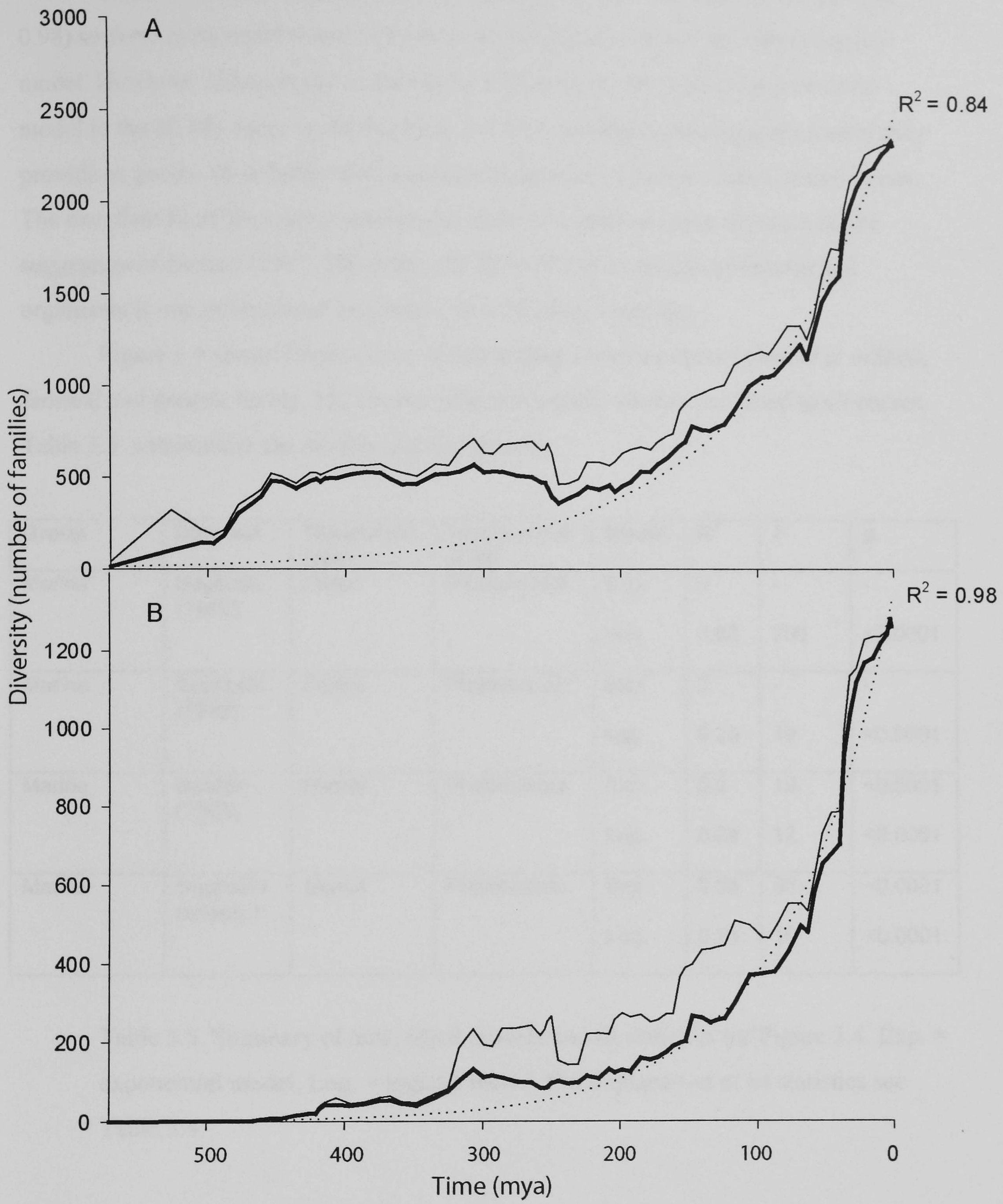


FIGURE 3.3. Phanerozoic global diversity curves with exponential model fitted. (A) All animal families. (B) Non-marine families. Data from the *Fossil Record 2* (Benton 1993). Bold line excludes uncertain families and singletons. Dotted line shows the fit of the exponential diversification model to the data, correlation coefficients are given for each fit.

The fit of the exponential model is excellent for the non-marine life curve (R^2 = 0.98) so there is no requirement to fit the additional parameter of the simple logistic model. However, although the correlation coefficient for the fit of the exponential model to the all life curve is also high (R^2 = 0.84) a multiple-phase logistic model may provide as good a fit or better than a single exponential equation - this is tested below. The excellent fit of the exponential model to the non-marine curve agrees with the suggestion of Benton (1997, 2000) that the diversification pattern of continental organisms is one of continual expansion up until the present day.

Figure 3.4 shows Phanerozoic global marine diversity curves plotted at ordinal, familial and generic levels. The exponential and logistic models are fitted to all curves. Table 3.5. summarises the models and fit statistics.

Group	Data set	Taxonomic level	Time period of fit	Model	R^2	*F*	*p*
Marine	Sepkoski (1992)	Order	Phanerozoic	Exp.	0	-	-
				Log.	0.83	200	<0.0001
Marine	Sepkoski (1992)	Family	Phanerozoic	Exp.	0	-	-
				Log.	0.33	19	<0.0001
Marine	Benton (1993)	Family	Phanerozoic	Exp.	0.2	19	<0.0001
				Log.	0.24	12	<0.0001
Marine	Sepkoski (unpub.)	Genus	Phanerozoic	Exp.	0.54	93	<0.0001
				Log.	0.21	10	<0.0001

Table 3.5. Summary of data, fitted models and fit statistics for Figure 3.4. Exp. = exponential model, Log. = logistic model. For explanation of fit statistics see Table 3.4.

The logistic equation provides a good description of the data at ordinal level, as discovered by Sepkoski (1978). At familial level, however, the single logistic model becomes inadequate as the long, ordinal-level diversity plateau from the Ordovician to the Recent is not evident (Sepkoski 1979). Similarly at generic level the simple logistic model is a poor fit. The exponential model displays the opposite trend. At ordinal level there is no fit; the same is true for the Sepkoski family data, but a poor fit is evident for

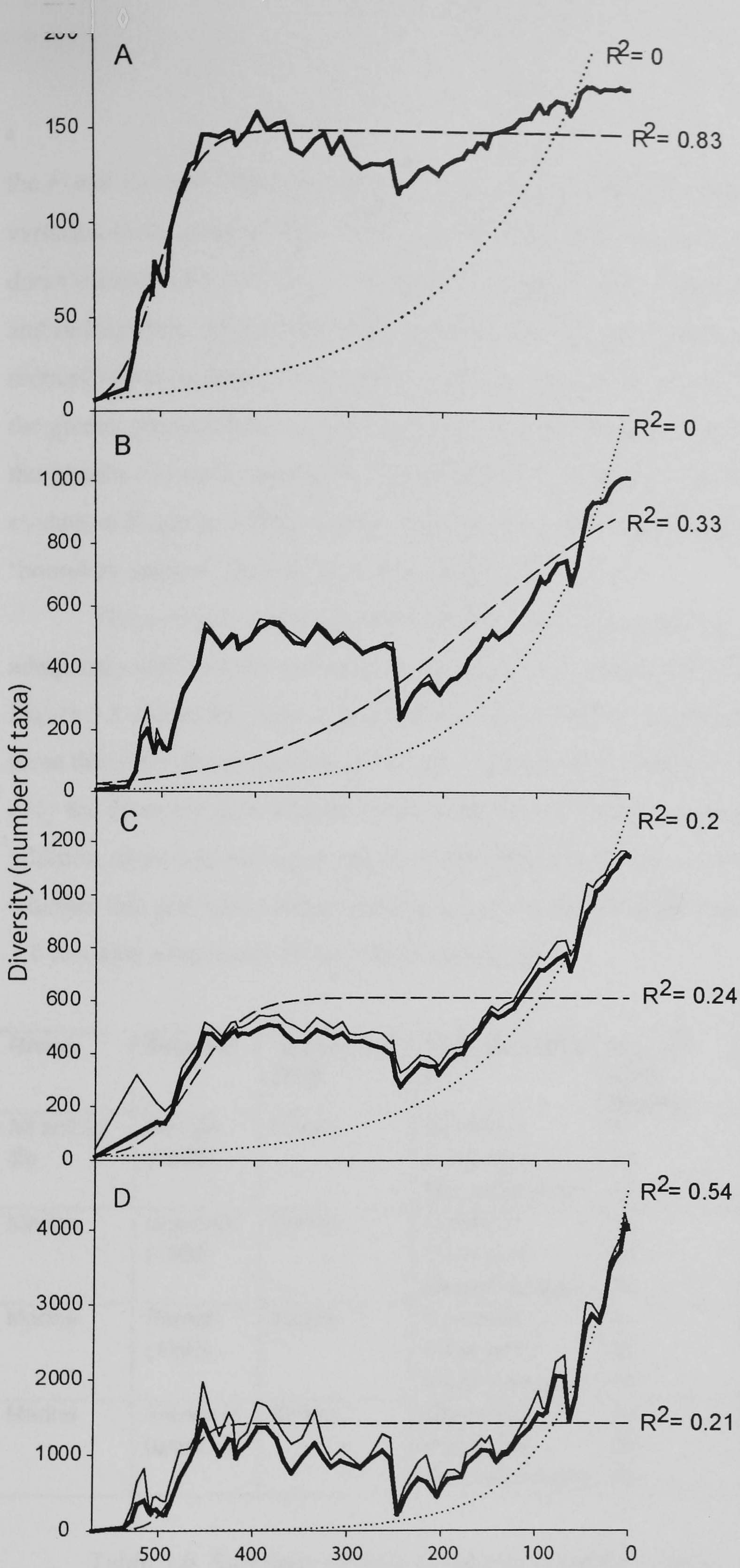


FIGURE 3.4. Phanerozoic marine diversity curves with exponential and logistic models fitted. (A) Marine orders. Data from Sepkoski (1992). (B) Marine families. Data from Sepkoski (1992). (C) Marine families. Data from Benton (1993). (D) Marine genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons. Dotted lines indicate the fit of the exponential model, dashed lines indicate the fit of the logistic model. Correlation coefficients are given for each fit.

the *Fossil Record 2* data. However, the exponential model describes over 50% of the variation in the generic data. This increase in the fit of the exponential model moving down taxonomic levels is due to the deterioration of the equilibria seen in the familial and ordinal data. At generic level the Palaeozoic plateau is still evident, but it is much reduced when compared to the later Mesozoic expansion, and difficult to discern due to the greater perturbations in generic diversity data (Sepkoski 1997). The general shape of the generic curve, in particular degradation of the Palaeozoic plateau, is similar to that evident in Foote's (2000a) marine Phanerozoic generic curve produced using the 'boundary crosser' method of summing diversity.

These results demonstrate that neither the exponential nor a single logistic model adequately explains the variation in marine diversity seen at familial and generic level. Figure 3.5 shows the marine diversity curves with three logistic equations fitted to the three diversity phase sections of the curve proposed by Sepkoski (1984). For simplicity only the diversity data with uncertain taxa and singletons removed has been plotted. In addition, three logistic equations have been fitted to the curve of all animal life to test whether this provides a better description of the data than the exponential model. Table 3.6 contains a summary of the statistical results.

Group	Data set	Taxonomic level	Time period of fit	No. of data points	R^2	*F*	*p*
All animal life	Benton (1993)	Family	Cambrian	5	0.96	25	0.039
			Palaeozoic	24	0.9	96	<0.0001
			Meso-Cenozoic	44	0.98	916	<0.0001
Marine	Sepkoski (1992)	Family	Cambrian	10	0.79	13	0.0043
			Palaeozoic	26	0.95	238	<0.0001
			Meso-Cenozoic	42	0.98	1021	<0.0001
Marine	Benton (1993)	Family	Cambrian	5	0.96	25	0.0392
			Palaeozoic	24	0.92	125	<0.0001
			Meso-Cenozoic	44	0.99	1675	<0.0001
Marine	Sepkoski (unpub.)	Genus	Cambrian	10	0.72	9	0.0118
			Palaeozoic	26	0.74	33	<0.0001
			Meso-Cenozoic	42	0.96	441	<0.0001

Table 3.6. Summary of data, fitted models and fit statistics for Figure 3.5. For explanation of fit statistics see Table 3.4. For time range definitions of the three phases see Section 3.2.3.

These best fit results of the logistic model to the three phase sections of the diversity curves have been used to determine the free parameters of the equations. Table 3.7 contains the parameter values for all the logistic fits shown in Figure 3.5. D_0, the initial diversity parameter, is constrained to equal the diversity level of the system at the start of the phase. r_0 and D_{eq} are the two free parameters derived from the model fit.

Group	Data set	Taxonomic level	Time period of fit	D_0	r_0	D_{eq}
All animal life	Benton (1993)	Family	Cambrian	13	0.051	193
			Palaeozoic	183	0.072	508
			Meso-Cenozoic	359	0.007	3.5×10^8
Marine	Sepkoski (1992)	Family	Cambrian	1	0.142	164
			Palaeozoic	141	0.071	505
			Meso-Cenozoic	238	0.009	1777
Marine	Benton (1993)	Family	Cambrian	13	0.051	192
			Palaeozoic	182	0.088	474
			Meso-Cenozoic	277	0.006	5218
Marine	Sepkoski (unpub.)	Genus	Cambrian	1	0.166	291
			Palaeozoic	233	0.106	1086
			Meso-Cenozoic	217	0.013	1.3×10^4

Table 3.7. Logistic model parameters for the three phases of Phanerozoic diversity. D_0 = initial diversity level (number of taxa), r_0 = initial diversification rate (net number of new taxa per lineage million years), D_{eq} = equilibrium diversity level (number of taxa).

The fit of the three logistic equations to the all animal life curve (Fig. 3.5A) is good, with each phase fit having an R^2 value of 0.9 or above. Therefore a three-phase logistic model seems to describe the diversification pattern of Phanerozoic animal life better than a single exponential model, which has an R^2 value of 0.84 (Fig. 3.3A and Table 3.4). However there are problems with the fits. Firstly the Cambrian phase model is only fitted to five data points, and this unreliability is reflected in the higher p value in Table 3.5 than those of the Palaeozoic and Meso-Cenozoic phases. Secondly, the logistic fit to the Meso-Cenozoic phase does not approach its equilibrium stage, as evidenced by the very high value for the all life, Meso-Cenozoic phase D_{eq} parameter given in Table 3.6. The prediction that animal life diversity will not achieve a future equilibrium until reaching a level of 3.5×10^8 families suggests that the exponential

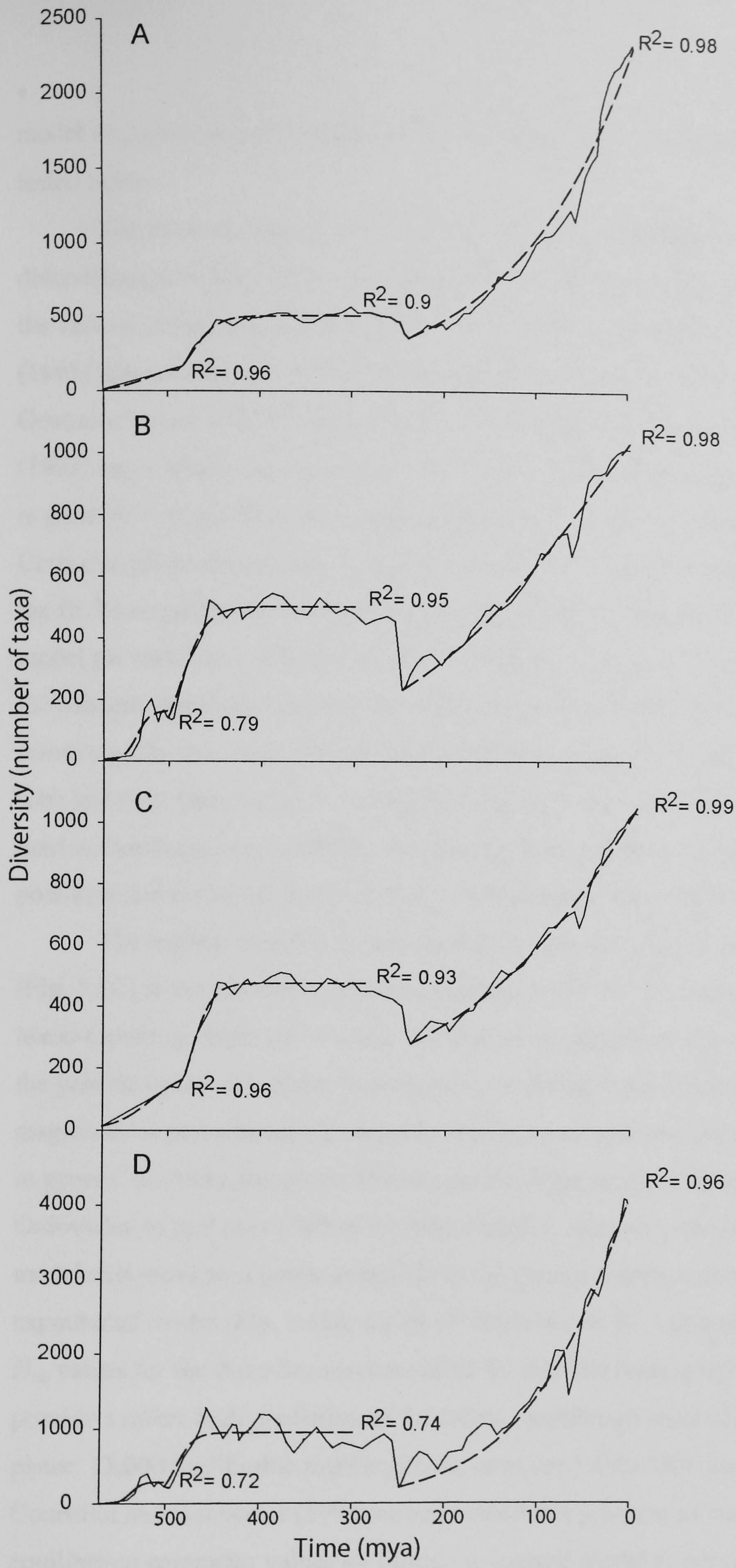


FIGURE 3.5. Phanerozoic diversity curves with three logistic equations fitted. (A) All animal life families. Data from Benton (1993). (B) Marine families. Data from Sepkoski (1992). (C) Marine families. Data from Benton (1993). (D) Marine genera. Data from Sepkoski (unpub.). Data excludes uncertain taxa and/or singletons. Dashed lines indicate the fit of the logistic model to the three periods indicated in the text. Correlation coefficients are given for each fit.

model may provide just as good a fit to the Meso-Cenozoic phase as the logistic. This is tested below.

The three logistic-phase model provides a good description of marine diversification at familial and generic level, with R^2 values for the fits of the equation to the various phases ranging from 0.72 to 0.99. Both the Sepkoski (1992) and Benton (1993) data curves (Fig. 3.5B & C) display an excellent fit for the Palaeozoic and Meso-Cenozoic phases with R^2 values >0.92. The fit to the Cambrian phase of the Sepkoski (1992) curve is less convincing ($R^2 = 0.79$), conversely that of the *Fossil Record 2* data is good ($R^2 = 0.96$). However, once again the *Fossil Record 2* data include only five Cambrian phase data points, reflected in a higher *p* value indicating less confidence in the fit. The equilibrium level parameter values (D_{eq}) for the three fits of the logistic model for each curve (Table 3.6) are reasonable for all phases, except perhaps that of the Modern phase described by the *Fossil Record 2* (Benton 1993) data. This predicts a future equilibrium level of 5218 fossilisable families in the world's oceans, compared with just over 1000 today. It is difficult to know if a five-fold increase in numbers of marine families is unreasonable, and this apparently high level may be an indication that post-Permian ocean life is diversifying exponentially rather than logistically.

The logistic model is an adequate description of generic marine diversification (Fig. 3.5C) in the Cambrian and later Palaeozoic ($R^2 <0.75$), and is an excellent fit to the Meso-Cenozoic phase ($R^2 = 0.96$). The reason for the poorer fit of the logistic model to the generic Palaeozoic phase than that seen at family level is due firstly to the greater magnitude of perturbations around the 'equilibrium' and secondly to the slight decline in generic diversity though the Plateau period, from nearly 1500 genera in the Mid-Ordovician to just over 1000 in the Mid-Permian. However, the three-phase logistic model still provides a better overall fit to the generic marine curve than the single exponential model (Fig. 3.4D), the fit of which has an R^2 value of only 0.54. Again the D_{eq} values for the three fits are reasonable for the Cambrian and Palaeozoic phases, but provide a rather high prediction of the future equilibrium level of the Meso-Cenozoic phase: 13,000 fossilisable marine genera, compared with 4000 known in the Recent. Courtillot and Gaudemer (1996) circumvented this problem of "meaningless" equilibrium parameter values by fitting the logistic model to not one, but three sections of the marine family data curve through the Meso-Cenozoic. However their Triassic fit was poorly constrained due to a low number of data points, and, as is shown above, the D_{eq} values for future marine family equilibrium levels are not unreasonable when the

logistic model is fitted to the complete Meso-Cenozoic curve and not just the Triassic – Cretaceous, as in the Courtillot and Gaudemer analysis. Finally, a more simple explanation for the predicted high future equilibrium levels is that the diversification of life in the oceans and on land since the Permian has in fact been exponential and not logistic. The fit of the exponential model to the Meso-Cenozoic phase of the all animal life and marine curves is shown in Table 3.8.

Group	Data set	Taxonomic level	Time period of fit	R^2	*F*	*p*	r_d
All animal life	Benton (1993)	Family	Meso-Cenozoic	0.98	1876	<0.0001	0.008
Marine	Sepkoski (1992)	Family	Meso-Cenozoic	0.96	876	<0.0001	0.006
Marine	Benton (1993)	Family	Meso-Cenozoic	0.99	2998	<0.0001	0.006
Marine	Sepkoski (unpub.)	Genus	Meso-Cenozoic	0.95	786	<0.0001	0.012

Table 3.8. Data and exponential model fit statistics for the Meso-Cenozoic phase. For explanation of fit statistics see Table 3.4. The value of the free parameter of the model, r_d (diversification rate), is given for each fit (units = number of new taxa per taxon standing diversity per million years).

Comparing these values with those for the logistic model fit to the Meso-Cenozoic phase (Tables 3.6, 3.7) shows that the exponential model provides as good a description of the data as the logistic in the case of the all animal life curve and the marine family level curve described by the *Fossil Record 2* data. It also has almost as good a fit as the logistic model for both the Sepkoski familial and generic curves. The diversification rate parameters (r_0 and r_d) are very similar for both models. Therefore the exponential model provides a good description of diversification since the Permian, without the additional parameter of the logistic model.

3.3.1.1. A model of Phanerozoic marine species diversity

The parameters derived from the fits of the three logistic equations to the familial and generic marine diversity curves (Table 3.7) have been used to calculate parameters defining a hypothetical species level curve. Table 3.9 contains the data used for these calculations and the resulting parameters for the species models.

Taxonomic level and dataset used	Cambrian phase			Palaeozoic phase			Meso-Cenozoic phase		
	D_0	r_0	D_{eq}	D_0	r_0	D_{eq}	D_0	r_0	D_{eq}
Family (Sepkoski 1992)	1	0.142	164	141	0.071	505	238	0.009	1777
Genera (Sepkoski unpub.)	1	0.166	291	233	0.106	1086	217	0.013	13000
% change family-genera:	0	16.9	77.4	65.2	49.3	115	-8.8	116.7	631.6
Species (model)	**1**	**0.194**	**516**	**385**	**0.158**	**2335**	**198**	**0.028**	**95104**

Table 3.9. Parameters derived for the three-phase logistic models. Models are fit to the familial and generic marine diversity curves. The initial diversity (D_0) parameter is not derived, but is set to the actual diversity at the start of each phase. The percentage change from family to genus level for each parameter is given, the generic values are then altered by this amount to give the species curve parameters. For definitions of parameters see Table 3.7.

The modelled species marine diversity curves are illustrated in Figure 3.6, with the empirical familial and generic curves for comparison. The non-perturbed solution curve (Fig. 3.6C) has a diversity pattern recognisable as the Phanerozoic marine curve. However the two plateaux apparent in the Cambrian and later Palaeozoic are much reduced compared to the sharp rise in species numbers after the end-Permian extinction. This extinction event itself is more severe than those seen at generic and familial level, with species numbers dropping from the equilibrium level of 2335 species in the Carboniferous to 198 in the Triassic, a 91.5% drop. This is consistent with the theory that plotting diversity at higher taxonomic levels dampens extinction events (Raup 1979b). Families are more likely to range through extinction events and therefore both the percentage and absolute numbers surviving are greater than those seen at generic and species level (cf. Jablonski & Raup 1995). The post-Permian rise in species numbers is dramatic, from 198 species to over 17 000 in the Recent (These figures are of course only modelling a sample of the total numbers of species present at any one time, as represented by the fossil record). Despite the Palaeozoic plateau being evident, the sharp Meso-Cenozoic rise causes the overall form of the curve to appear exponential. The plateau is even less apparent in the curve modelled with perturbations (Fig. 3.6D). The fluctuations in diversity though the Palaeozoic detract from the appearance of equilibrium.

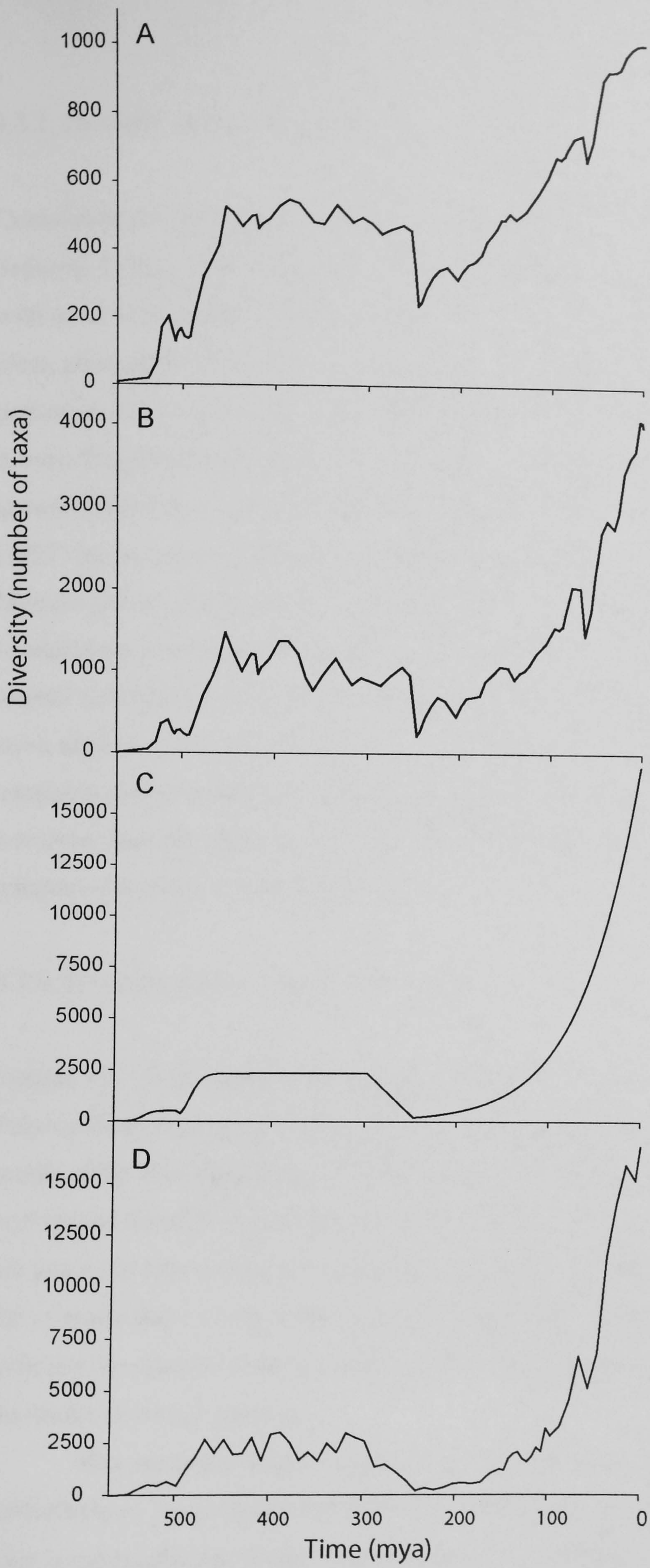


FIGURE 3.6. Empirical and modeled Phanerozoic global diversity curves. (A) Marine families. Data from Sepkoski (1992). (B) Marine genera. Data from Sepkoski (unpub.). Empirical data excludes singletons. (C) Marine species diversity curve modelled using three logistic equations derived from the family and genus data logistic parameters. (D) Species curve modelled to include diversity perturbations.

3.3.2. Diversity curves – three faunas

Cumulative and individual diversity curves representing the three evolutionary faunas of Sepkoski (1981) at familial and generic level are shown in Figure 3.7. The results agree with those of Sepkoski (1997): there is a reasonable level of similarity between the plots, although, as with the complete marine curve, the generic data contain more perturbations. In particular, genera show greater drops in diversity at mass extinction events. The Modern fauna at genus level also displays a markedly more exponential growth pattern than at family level. This difference was not identified by Sepkoski (1997) due to the exclusion of Recent genera, which has a damping effect on the Modern generic diversification pattern. These results suggest that the Modern evolutionary fauna does not conform to the logistic diversification model. However, the overall similarities among the curves suggests that genera within classes display the same kind of 'diversity association' as families within classes, with large groups of unrelated genera waxing and waning in diversity in a synchronised manner. This result, however, does not provide evidence for the ecological significance of macroevolutionary diversity associations.

3.3.3. Diversity curves – major Palaeozoic classes

Figures 3.8 – 3.16 contain the diversity curves for the ten dominant classes of the Palaeozoic plateau period (Ordovician – Carboniferous). Similarity between the curves produced by the Sepkoski (1992) and Benton (1993) datasets is high: the majority of the ordinal and familial plots display a similar pattern across datasets. The ordinal curves are generally less similar due to the low numbers of orders within some of the classes, for example those of Class Anthozoa (Fig. 3.8A & B) where a slight discrepancy between the datasets in the numbers of orders through time produces two very dissimilar diversity patterns.

Moving down the taxonomic levels the data curves become more prone to perturbations. Large jumps and dips in diversity are particularly evident at generic level. This is especially true for the smaller classes, e.g. Cephalopoda (Fig. 3.11E) and 'Stelleroidea' (Fig. 3.15E). This illustrates the tendency of higher taxonomic levels to 'smooth out' diversity patterns (Sepkoski 1978). Comparability among the patterns displayed at differing taxonomic levels varies. Some, e.g. Articulata (Fig. 3.9) and

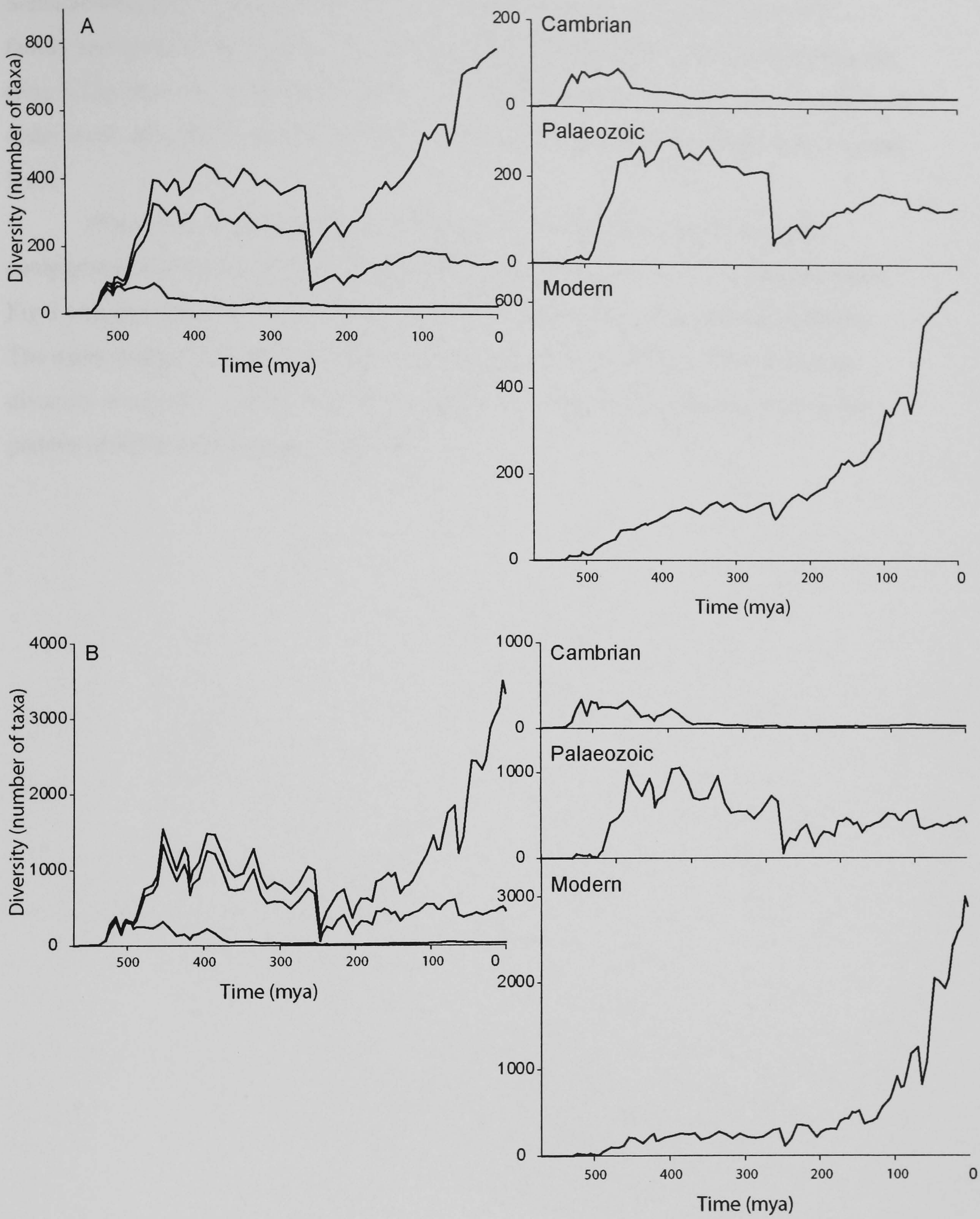


FIGURE 3.7. Phanerozoic global diversity curves for the three evolutionary faunas of Sepkoski (1984). (A) Cumulative and individual curves for marine families. Data from Sepkoski (1992). (B) Cumulative and individual curves for marine genera. Data from Sepkoski (unpub.). Data excludes singletons.

Stenolaemata (Fig. 3.16), show reasonable similarity between the curves at order, family and genus level. Conversely others, such as Bivalvia (Fig. 3.10) and Gastropoda (Fig. 3.13), show only a weak correlation. Bivalvia displays a strongly logistic pattern at order level, an additive pattern at family level, and an exponential growth curve at genus level.

Where classes have an obvious 'plateau' or dominance in the Palaeozoic compared to later periods (e.g. Articulata, Fig. 3.9; Crinoidea, Fig. 3.12; Stenolaemata, Fig 3.16), this feature of the curve remains fairly robust at all three taxonomic levels. The main change from order through to genera data is an increase in fluctuations in diversity around the 'equilibrium' level, as clearly evident in the Palaeozoic diversity plateau of the Stenolaemates (Fig. 3.16).

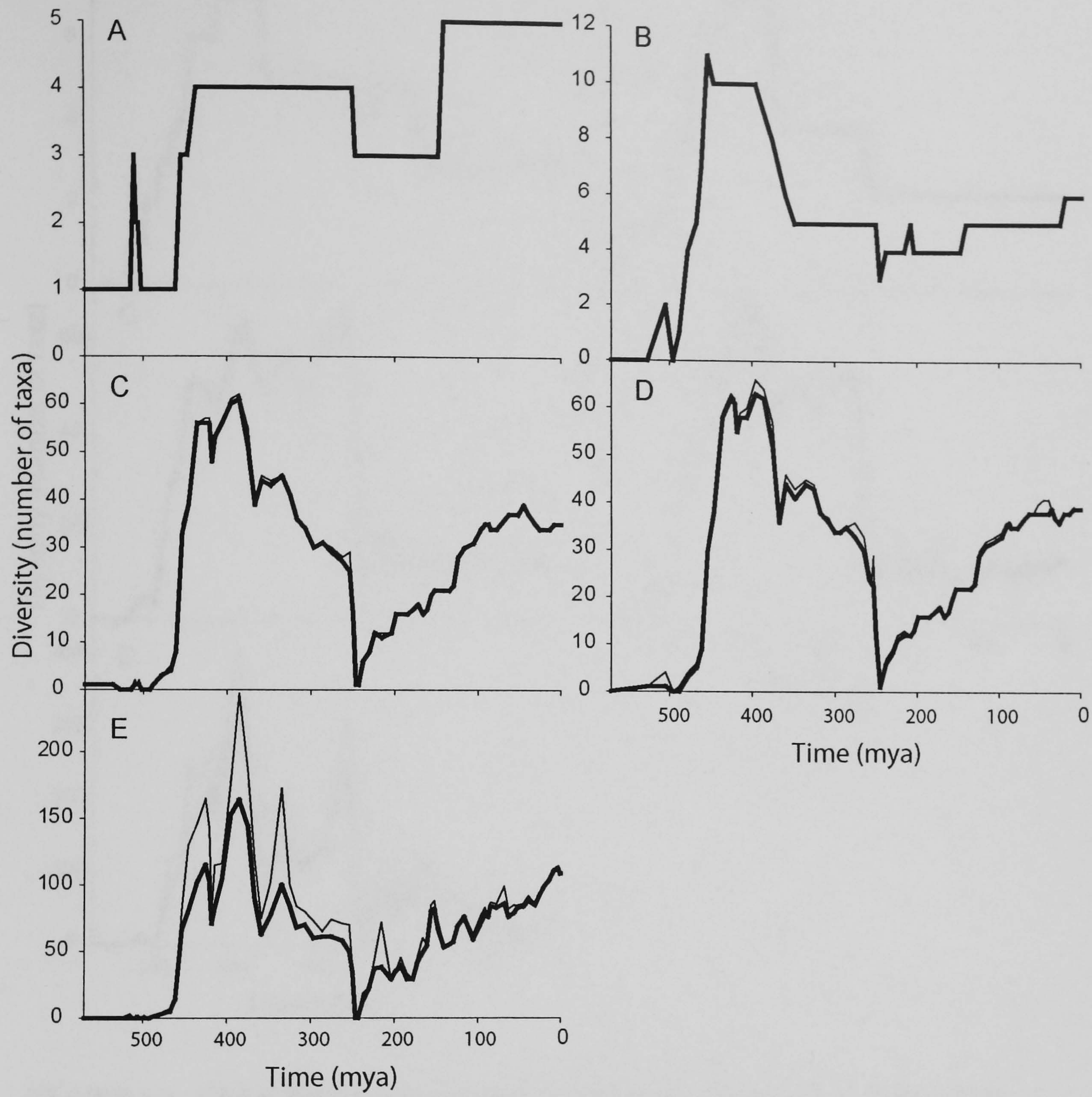


FIGURE 3.8. Global Phanerozoic diversity curves: Class Anthozoa. (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

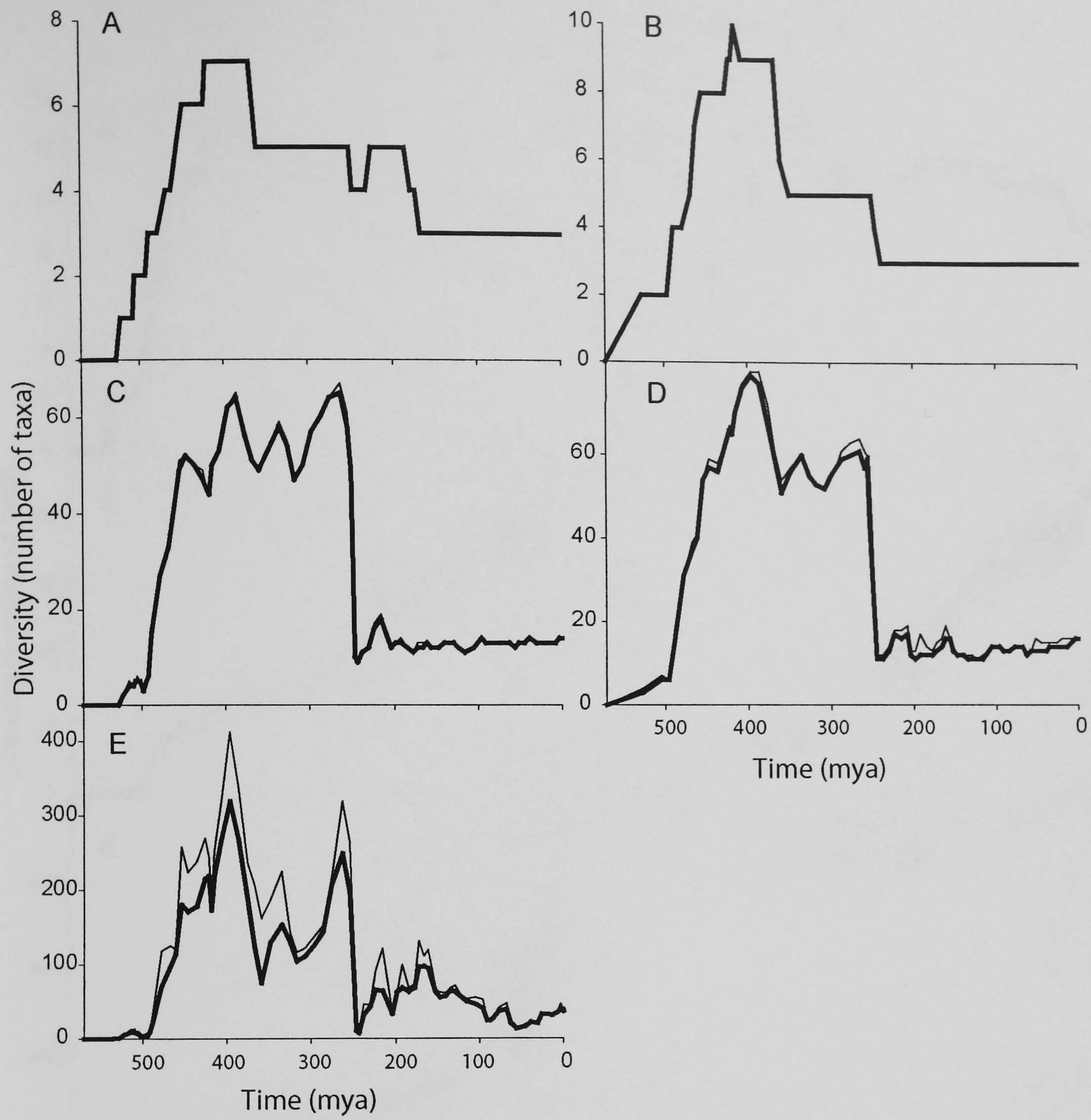


FIGURE 3.9. Global Phanerozoic diversity curves: Class Articulata. (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

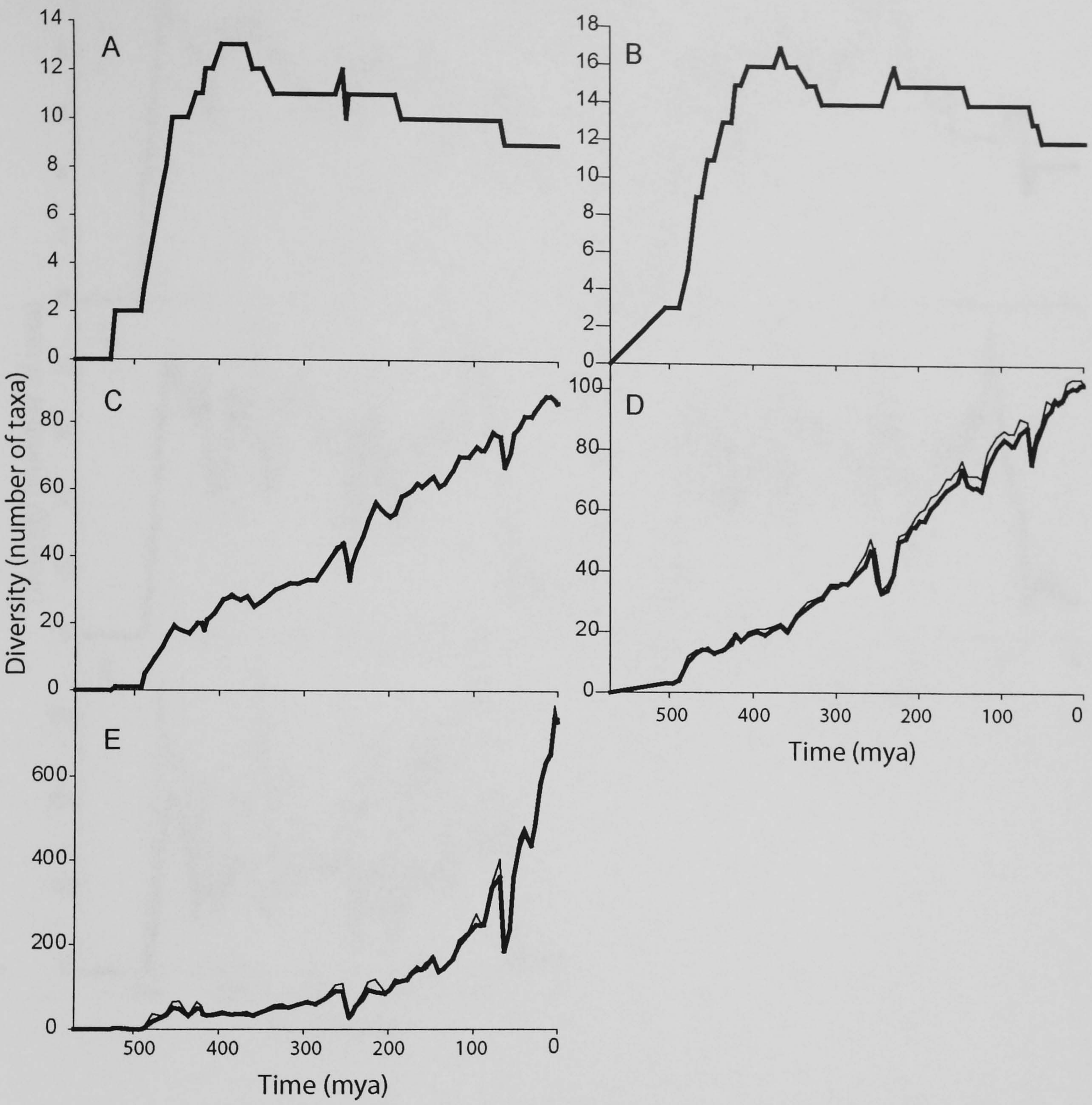


FIGURE 3.10. Global Phanerozoic diversity curves: Class Bivalvia. (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

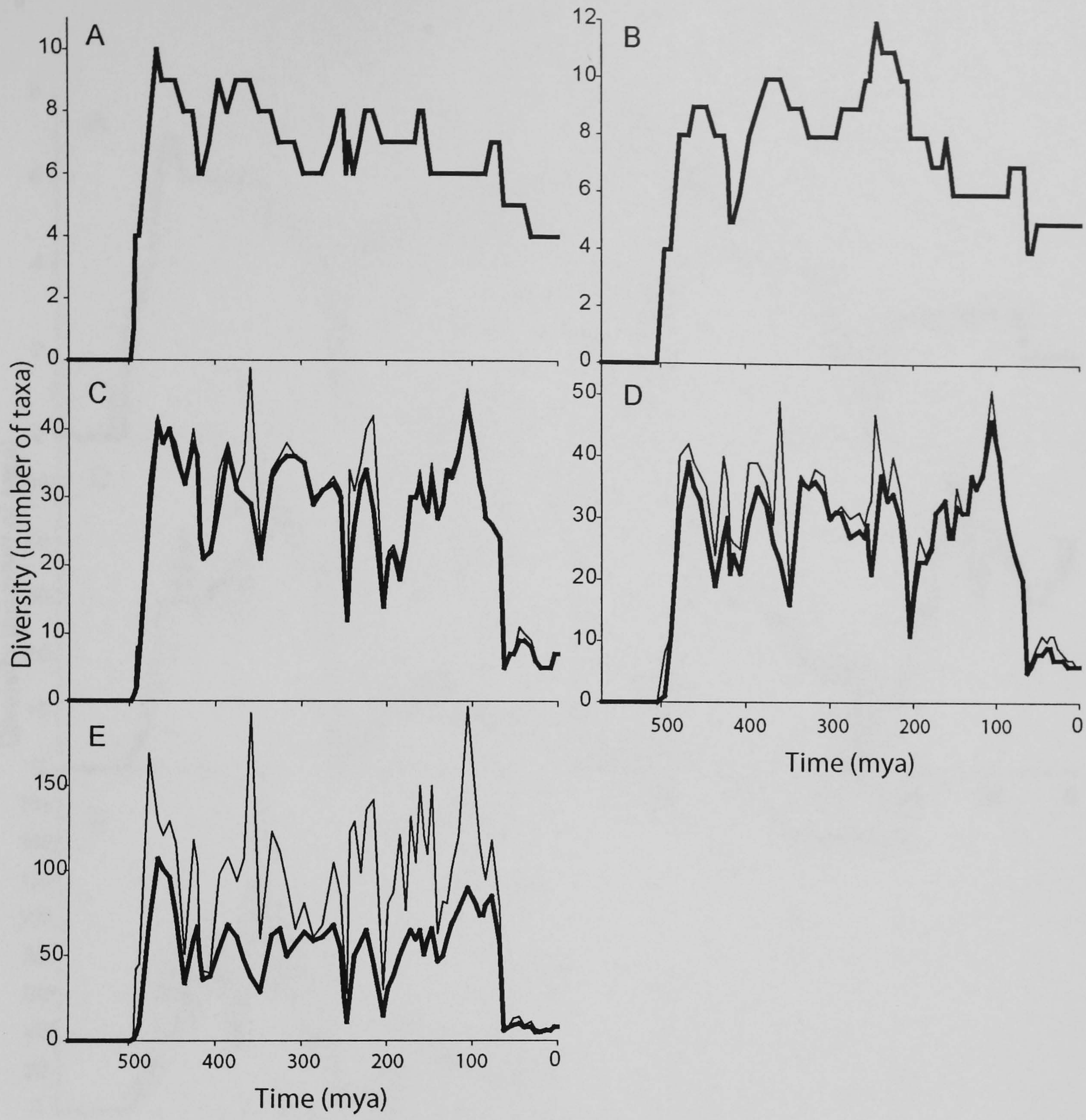


FIGURE 3.11. Global Phanerozoic diversity curves: Class Cephalopoda. (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

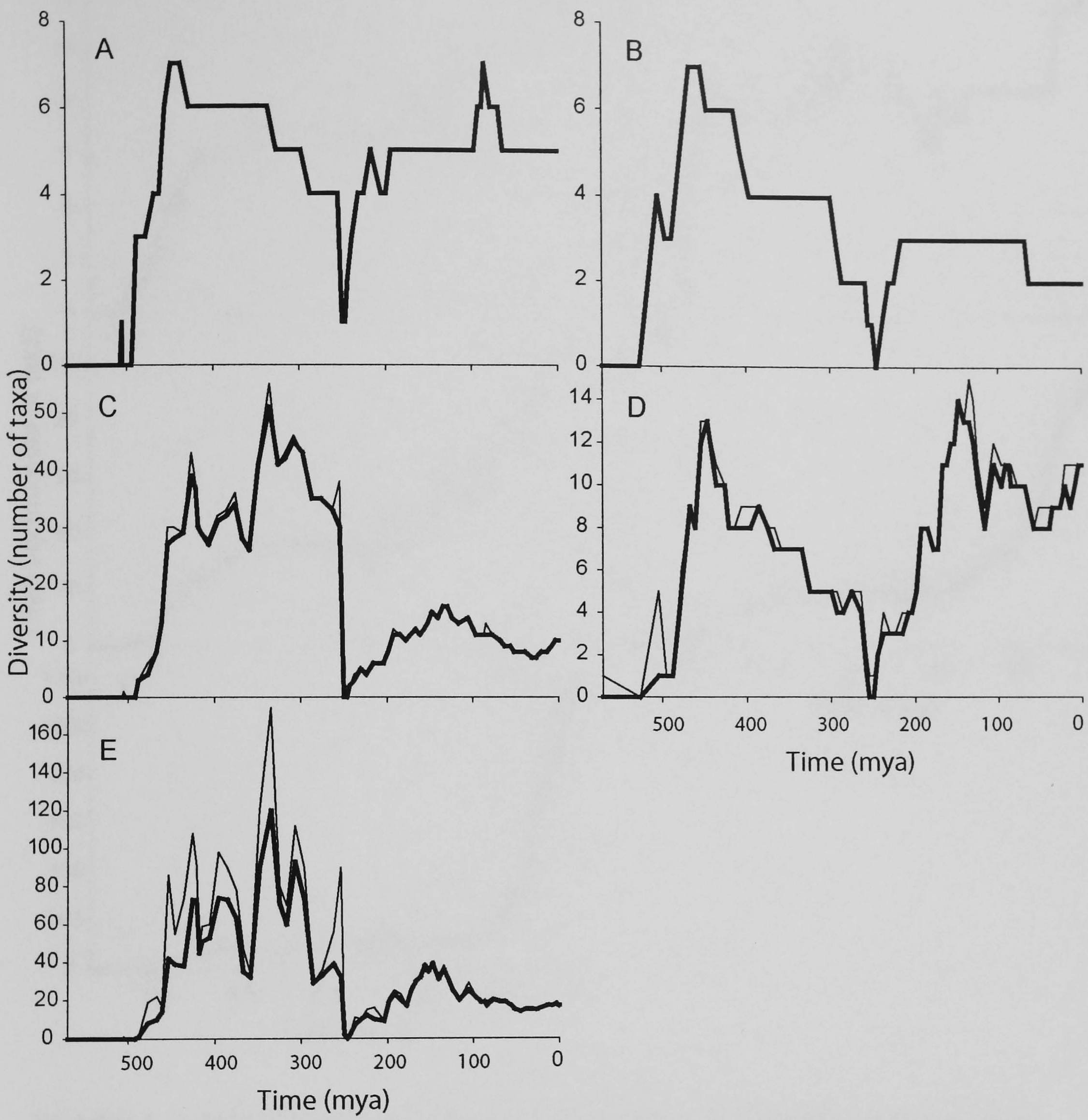


FIGURE 3.12. Global Phanerozoic diversity curves: Class Crinoidea. (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

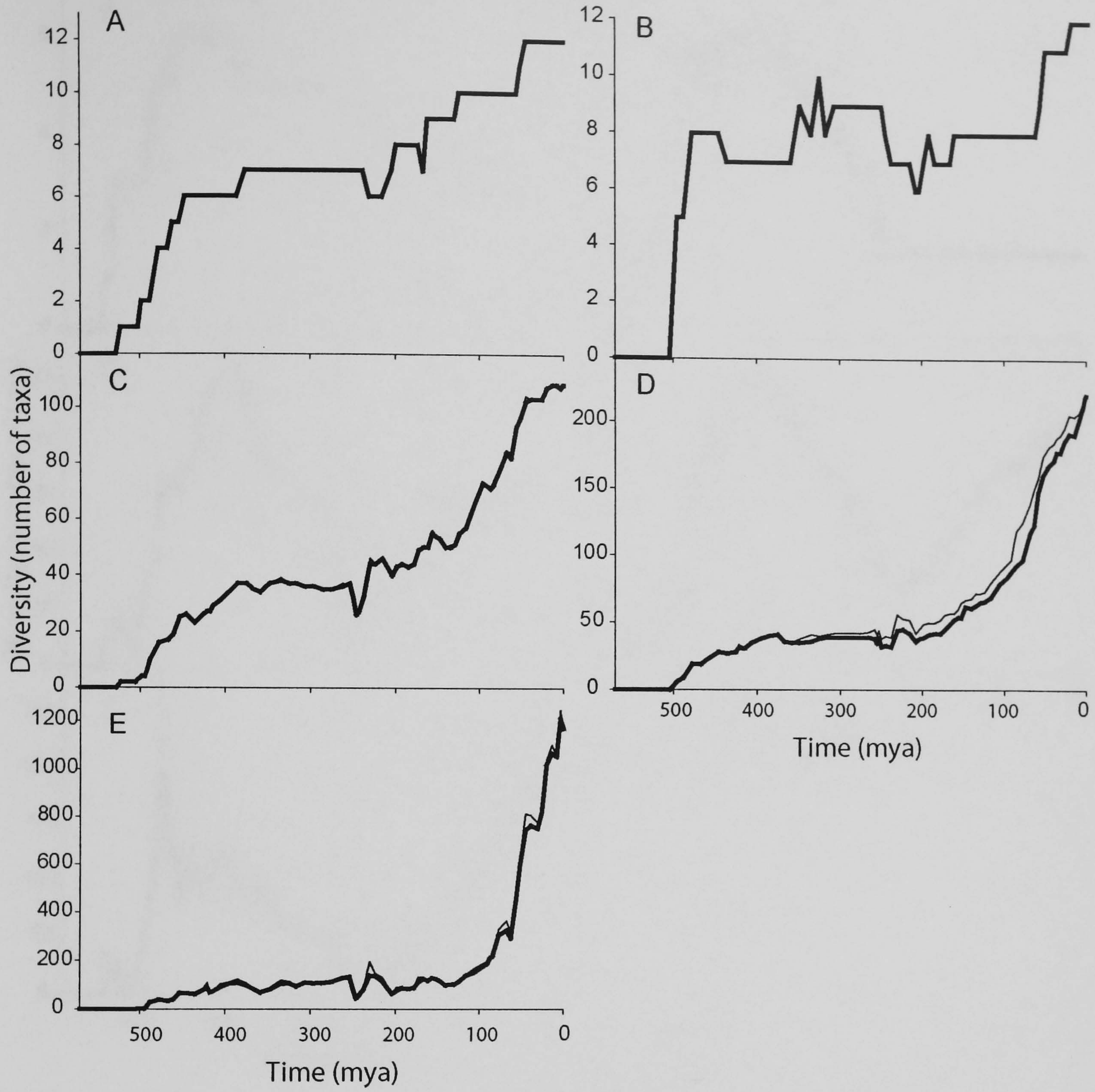


FIGURE 3.13. Global Phanerozoic diversity curves: Class Gastropoda (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

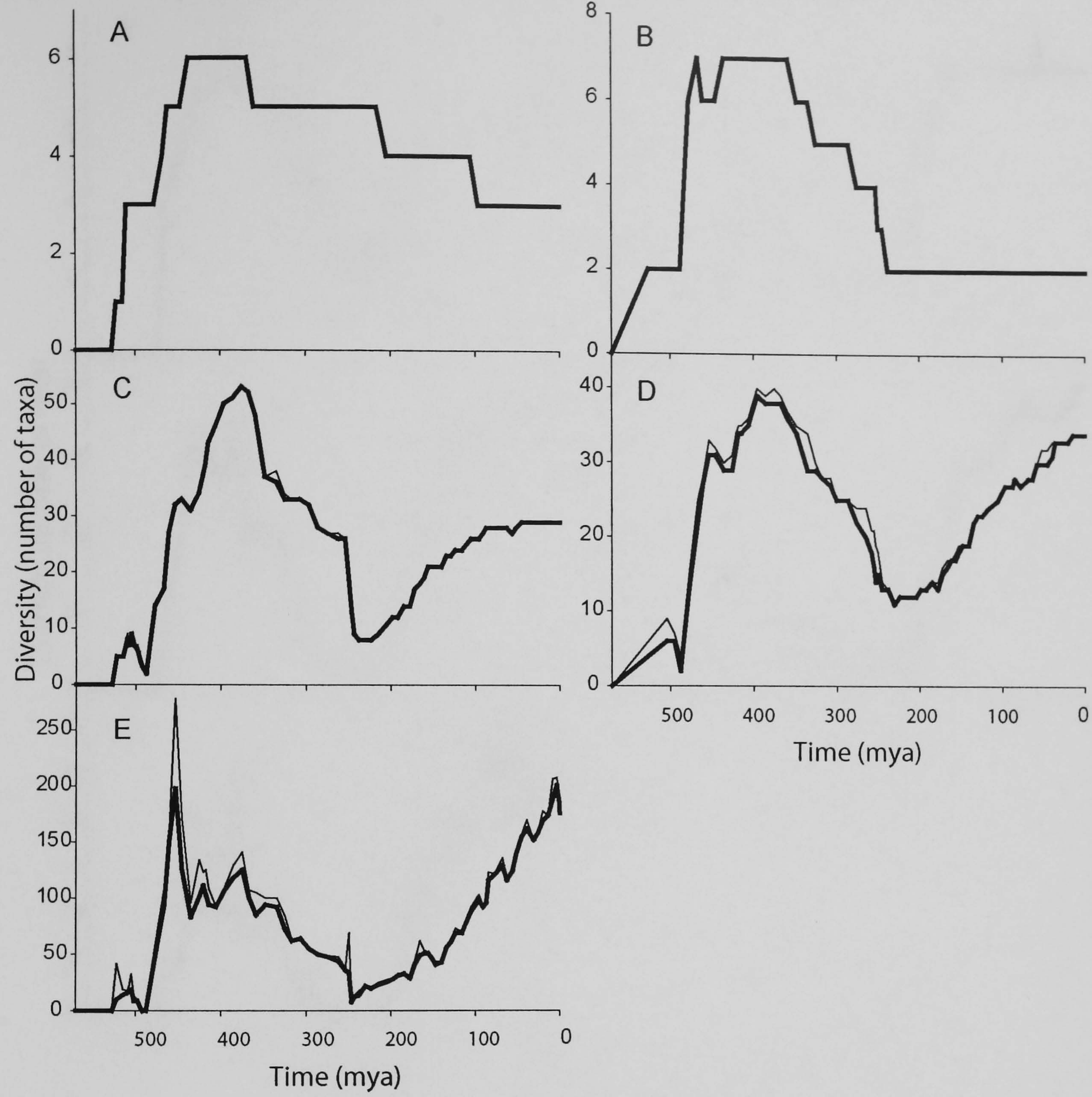


FIGURE 3.14. Global Phanerozoic diversity curves: Class Ostracoda (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

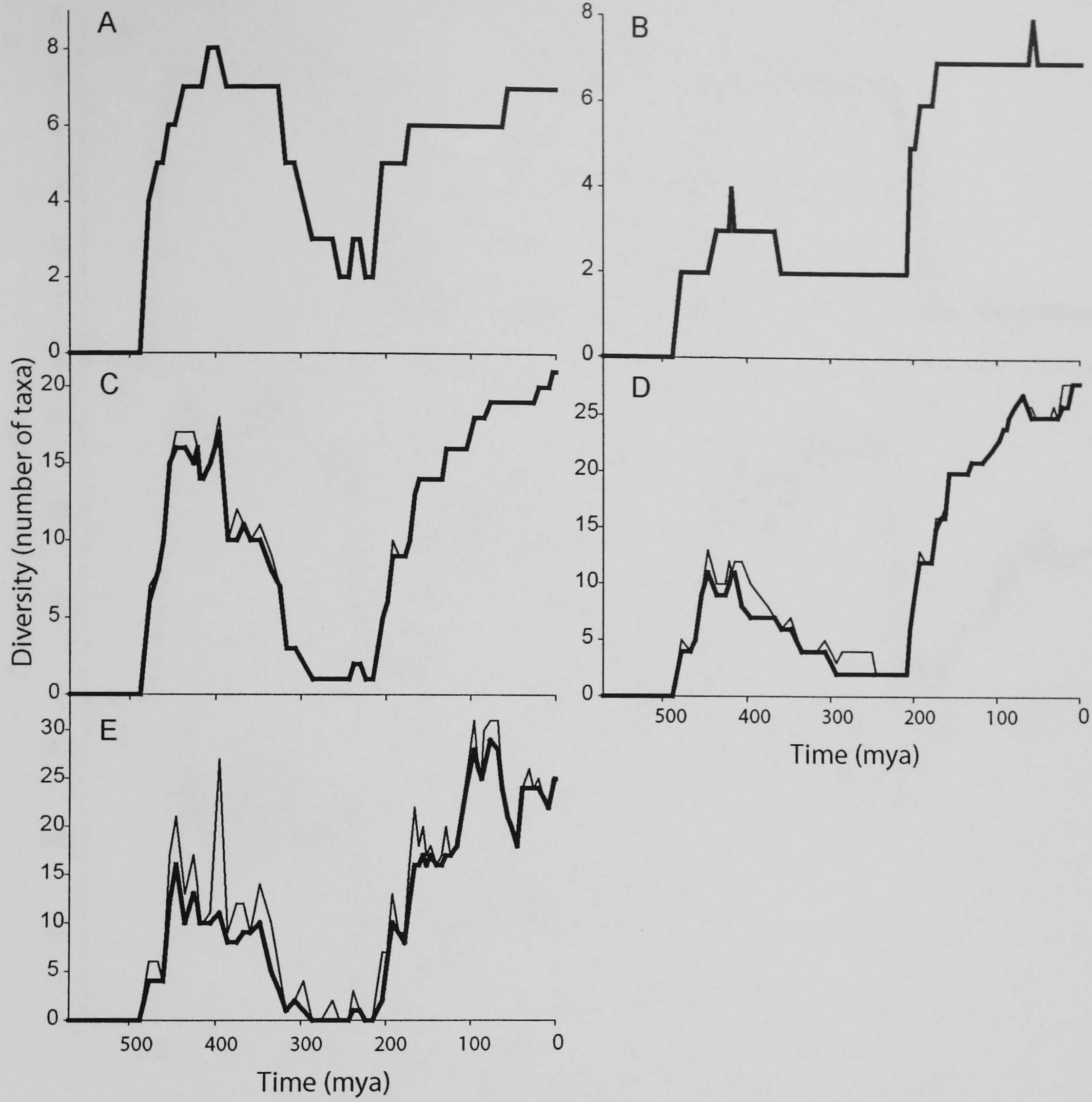


FIGURE 3.15. Global Phanerozoic diversity curves: Class 'Stellleroidea' (Asteroidea & Ophiuroidea) (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

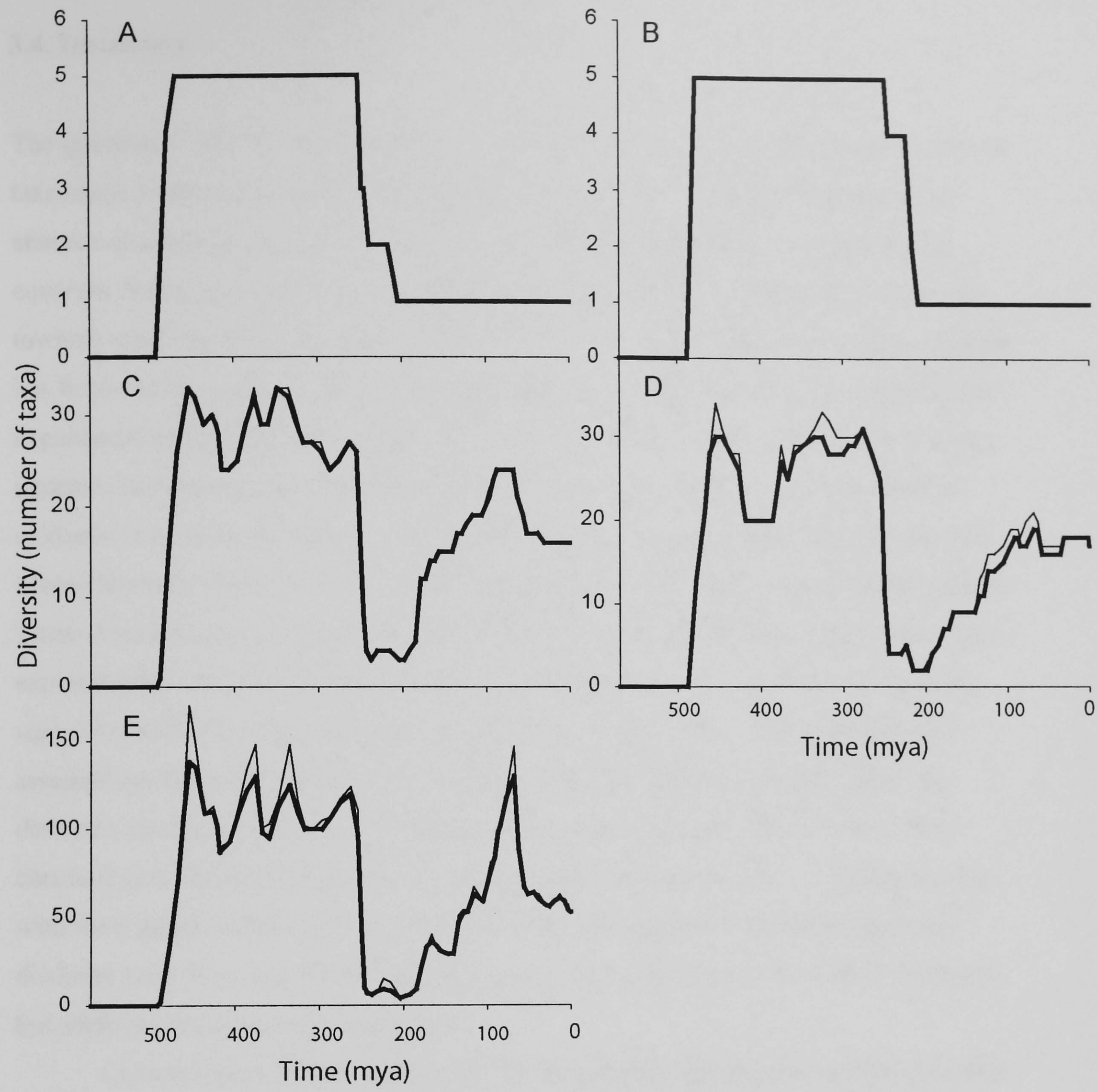


FIGURE 3.16. Global Phanerozoic diversity curves: Class Stenolaemata (A) Orders. Data from Sepkoski (1992) (B) Orders. Data from Benton (1993) (C) Families. Data from Sepkoski (1992). (D) Families. Data from Benton (1993). (E) Genera. Data from Sepkoski (unpub.). Bold lines exclude uncertain taxa and/or singletons.

3.4. Discussion

The question of whether the convention of plotting Phanerozoic diversity curves at high taxonomic levels is representative of the species pattern is difficult to answer in the absence of adequate species-level data. The combination of empirical data plotting, equation fitting, and simple species diversity modelling presented here goes some way towards resolving this issue. The suggestion of Benton (1997, 2000) that continental life has followed an expansive diversification pattern is verified by the results of fitting the exponential model to the non-marine data curve. Conversely, the all life curve displays a pattern more adequately described by a multiple-phase logistic model, though this evidence is weakened by the low number of Cambrian data points and the fact that the Meso-Cenozoic data are an excellent fit to the exponential model as well as the logistic. There is no evidence to suggest that familial life has diversified logistically rather than exponentially since the Permian, nor that marine or continental diversity are showing signs of reaching new equilibrium levels. Newman and Sibani (1999), using simple assumptions about the nature of diversification and extinction of taxa through time, derived a variety of constraints on the possible form of diversification trends. They conclude that taxonomic diversity can increase at most only linearly, a finding at odds with the exponential model. They note, however, that the curve for marine familial diversity does fit an exponential function reasonably (although no fit statistic is given), but attribute this fit to noise in the data.

Unfortunately, for non-marine life the exponential and logistic models currently cannot be tested at taxonomic levels lower than families due to the absence of adequate data. The Sepkoski generic database has allowed the question to be addressed for diversification in the marine realm. Plots at ordinal, familial and generic level show that taxonomic level does have an effect on the perceived diversification pattern: the single logistic model reduces in its goodness-of-fit from ordinal to generic data, while conversely the exponential model improves. Neither, however, provides as good a description of the marine data as the three logistic-phase equations, although once again the goodness-of-fit of these equations reduce from familial to generic level. In addition the problem of the low number of Cambrian data points, and the excellent fit of the exponential model to the Meso-Cenozoic phase, demonstrate that the post-Cambrian Palaeozoic pattern remains the most convincing evidence for logistic diversification. Courtillot and Gaudemer (1996) did not attempt to fit a Cambrian phase equation;

instead they included the Cambrian data in their Palaeozoic fit of the logistic model at family level. They also fitted multiple logistic equations to the Meso-Cenozoic data, but here a single logistic or exponential equation provides an excellent fit to this section of the curve. Courtillot and Gaudemer's rejection of 'meaningless' parameter values presupposes an upper diversity limit to any future equilibrium, if indeed such an equilibrium need be assumed at all. When the marine diversity curve is separated into the three 'evolutionary faunas' of Sepkoski (1981, 1984) the results are similar to those of the complete dataset plots – there is reasonable similarity between familial and generic curves, although the Modern fauna shows a strongly exponential growth curve at generic level, and the Palaeozoic fauna displays a reduced diversity plateau with many perturbations detracting from the appearance of equilibrium.

Therefore, the overall trend from the plots of marine diversity at ordinal, familial and generic level is one of decreasing dominance of the curve's logistic elements, most notably the Palaeozoic plateau, moving down the taxonomic hierarchy, and of an increasingly exponential form of the Phanerozoic pattern taken as a whole. The results corroborate the theory that higher taxonomic ranks become established early in the history of a group, while lower ranks gradually appear in increasing numbers as the group ages (Raup 1983); also the prediction of Sepkoski (1984) that the perceived increase in familial diversity in younger geological periods underestimates the actual increase in species diversity. These trends are demonstrated by the simple model of Phanerozoic marine species diversification. The resulting species diversity curves, both with and without perturbations, show the logistic phases of the Cambrian and Palaeozoic significantly reduced in magnitude relative to the sharp rise in species numbers in the Meso-Cenozoic, which reaches over 17,000 species in the Recent. This figure is not an estimation of the numbers of extant marine species, but rather of the number expected to be found as a fossilised sample of the Recent biota. Briggs (1994) gives an upper estimation of 171,000 extant marine species (excluding vascular plants and algae), so the model predicts a future fossil record sample of approximately 10% of marine biota in the Recent. The dominance of the logistic phases in the species model is reduced to such an extent that the overall curve has an exponential form. This could be an artefact of poor sampling at generic level, where fossil genera are decreasingly likely to be sampled with increasing distance back through geological time. The model methodology would magnify this effect in the species curve. The generic data, however, have been interpreted as providing a clear biodiversity signal (Sepkoski 1996b, 1997),

are considered robust enough to have been used in several recent biodiversity studies (Kirchner and Weil 2000a, b; Foote 2000a, b, 2001), and the change in pattern between family and generic curves has been accepted as a real feature of diversity at differing taxonomic levels (Benton 1997, 2000). The species model demonstrates that an expansive growth pattern can be constructed from individual logistic elements. Hence, if the importance of the Palaeozoic plateau is reduced from generic level to species level to the same extent as it is from families to genera, the overall diversification pattern of life through the Phanerozoic appears exponential, as suggested by Benton (1997, 2000) and by the species models of Signor (1985).

The problem of correlation among diversity patterns at different taxonomic levels becomes more acute when smaller groups of organisms are under analysis, as is shown by the plots of important Palaeozoic marine classes. Those groups with Palaeozoic dominance display a reasonably strong similarity among diversity plots at ordinal, familial and generic level, with plateau structures in particular being robust elements of the patterns, although with greater fluctuations around the equilibrium level. However, classes with post-Palaeozoic dominance (e.g. Bivalvia, Gastropoda) have a much poorer match among ordinal, familial and generic level plots. These diversity patterns again strongly demonstrate the tendency for large numbers of higher taxa to become established early in a group's history (Raup 1983) while lower rank taxa increase in number more slowly. A good example is the long plateau in bivalve diversity at ordinal level, which is reduced to exponential growth when generic numbers are analysed. Therefore, any diversity pattern evident at familial and ordinal level may be a distortion of the true pattern and not a reliable indicator of the growth dynamics of the group.

The results presented here investigate the trends in standing diversity through time using data of differing taxonomic levels, and with emphasis placed on the shape of the curves and any apparent diversity equilibria. To more fully understand the nature of the underlying diversity dynamics governing the form of the data, *rates* of origination and extinction though time must be analysed, and the effect of taxonomic level on these rates investigated. This is done in Chapter 5.

3.5. Conclusions

- In the absence of adequate species-level data, the hypothesis that the Palaeozoic plateau in Phanerozoic marine diversity is an artefact of taxonomic level cannot be disproved. The results presented here, however, confirming the presence of a diversity equilibrium at ordinal, familial and generic level, suggest that the plateau is real. The importance of the plateau as a defining feature of the Phanerozoic marine curve is reduced from familial to generic level due to a relatively lower magnitude, greater fluctuations in diversity around the equilibrium, and a strongly exponential post-Permian growth pattern. The question of why there was such an equilibrium during the Palaeozoic, but not after, requires further investigation.
- A species-level Phanerozoic marine diversity curve, modelled as a continuation of the trends existing between the familial and generic data, suggests that the Palaeozoic plateau is greatly reduced in relative magnitude compared to the large Meso-Cenozoic rise in species numbers, and that species diversification as a whole appears exponential. Therefore, it is proposed that the gross pattern of species diversification may be conceived as an overall exponential growth curve, but consisting of multiple logistic elements – i.e. a Cambrian rise and plateau, an Ordovician rise and later Palaeozoic plateau, and a Meso-Cenozoic rise. There is no evidence for a third plateau occurring in the near future.
- Smaller groups, e.g. classes, have diversity patterns less robust to plotting at higher taxonomic levels. In particular groups with Meso-Cenozoic dominance display distorted patterns at order and family level, due to the tendency for higher ranked taxa to be established early in a group's history.
- Continental familial life displays a strongly exponential growth pattern. The all life data display good fits to the three logistic phase equations, but the fit of the Cambrian phase is weakened by the low number of data points, and the Meso-Cenozoic phase fits an exponential model as strongly as the logistic.

CHAPTER 4. THE PALAEOZOIC PLATEAU – A STOCHASTIC STRUCTURE?

4.1. Introduction

The logistic model of biodiversification (Sepkoski 1978, 1979, 1984) is an attempt to explain the pattern of Phanerozoic diversity using a single set of general laws with deterministic ecological causes. The coupled logistic equations of the model describe the growth and equilibrium stages of a diversity system in the context of diversity damping, where ecological constraints such as inter-clade competition result in the slowing and eventual halt of net diversification. The Palaeozoic diversity plateau apparent in the marine family diversity curve (Fig. 4.1) is the strongest evidence for the logistic and other equilibrium models, although its significance has been questioned. Empirical (Benton 1997, 2001) and theoretical (Signor 1985) studies have suggested that the plateau breaks down to an exponential growth curve when diversity is plotted at the taxonomic level of genus and species.

Hoffman (1986, 1989) proposed an alternative 'neutral model' of biodiversification: probabilities of species origination and extinction are not governed by diversity dependence or any other over-arching biological law, but vary independently of one another, randomly over time. Hence the resulting overall pattern of change in diversity is a summation of millions of individual, independent species-level events which Hoffman likened to a statistical double random walk, one of speciation, the other of extinction. He compared the empirical pattern of biotic diversification in the Phanerozoic to simulations generated by the neutral model (Hoffman and Ghiold 1985; Hoffman and Fenster 1986), and concluded that the pattern is indistinguishable from randomness.

The extent to which the turnover of species and higher taxa can be viewed as a stochastic process has been investigated in several computer analyses. Raup et al. (1973; Raup 1977) used a stochastic simulation based upon an assumption of equilibrium diversification to test the possibility that some aspects of the fossil record behave as random variables. However this simulation used a greater number of deterministic parameters than Hoffman's. Origination and extinction rates were initially set at unequal values in the Raup et al. model, with diversity damping being achieved by reducing origination rates to equal those of extinction at a pre-defined point in the time-series.

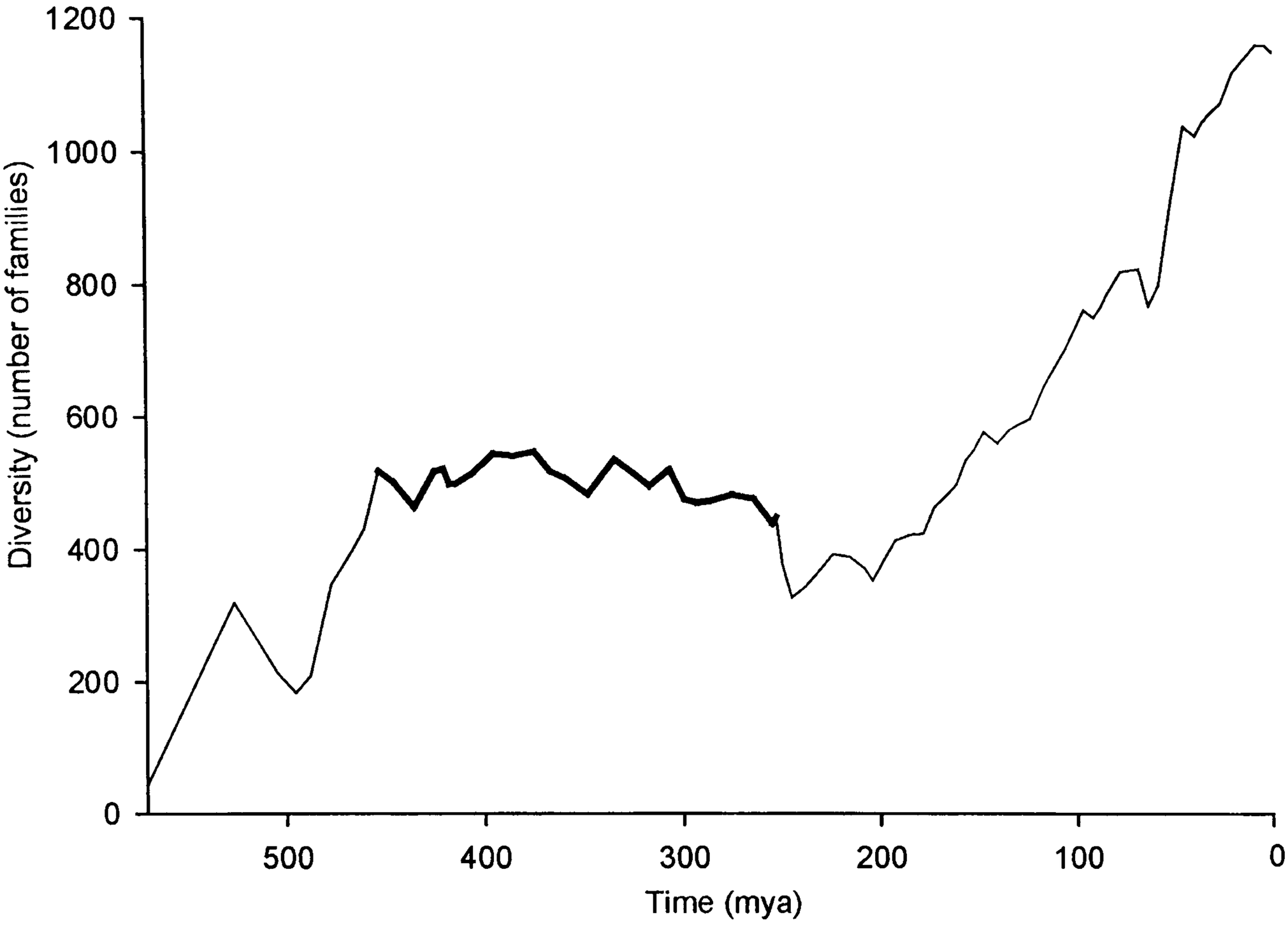


Figure 4.1. The Phanerozoic marine diversity curve plotted at familial level. Data from the *Fossil Record 2* data set (Benton 1993). The Palaeozoic plateau in diversity, running from the Caradoc to the Kungurian - approximately 200 myr, is shown by the bold section of the curve.

This damping produced a dynamic-equilibrium within the model, which could be either loosely or tightly constrained. Gould et al. (1977) used the same simulation to investigate the nature of clade shape. In this analysis, however, both equilibrium, with damped origination rates, and non-equilibrium diversity patterns were generated. Origination and extinction rates in the non-equilibrium simulation were equal and unchanging throughout the program run, i.e. a true random walk. Gould et al. (1979) concluded that many clade topologies that appear to have deterministic causes, e.g. the 'double wedge' shapes of purported competitive displacements, can be generated by random processes.

These results suggest that stochastic processes are an appropriate null model for clade dynamics. Further studies have demonstrated significant departures from an expected random pattern when comparing stochastically generated evolutionary patterns with real ones (e.g. Flessa and Levinton 1975; Stanley et al. 1981; Ward and Signor 1985; Pearson 1998), and when comparing present-day extinction trends with a phylogenetically random extinction model (Purvis et al. 2000). There are, however, reasons to question the use of stochastic simulations. The probabilities (origination and extinction rates) that are used to generate the random diversity patterns lie within certain limits, limits which themselves must have causes in the real world (Kemp 1999). Therefore it could be argued that they are deterministic parameters, controlling the topology of the resulting diversity patterns. Indeed the similarity between stochastic curves generated with probabilities taken from actual fossil data, and real Phanerozoic diversity curves has been used as a source of evidence for the equilibrium model (Sepkoski 1978). Hence the most genuinely stochastic models are those which use the smallest number of generating parameters (Raup 1977).

It has been shown that a true 'random walk', with origination and extinction probabilities set as equal and without any limiting parameters such as diversity damping, can simulate many of the features we associate with clade diversification, such as jumps, trends and irregular cycles (Bookstein 1987). Przeworski and Wall (1998) even suggested that the fossil record as a whole can be interpreted as having been drawn from a probability distribution of outcomes, rather than displaying any underlying deterministic model. Certainly an understanding of the stochastic nature of biodiversity patterns is required before any biological or ecological significance can be attributed to a particular diversity curve structure such as the Palaeozoic plateau.

4.2. Analysis methods

4.2.1. Use of random walk simulations

A random walk is a type of Markov chain, that is a sequence of events where each event is partly dependent upon the outcome of previous ones, and partly upon a random process. Figure 4.2 gives examples of 'coin flipping' random walks produced by computer random number generators. For each point along the horizontal axes shown in Figure 4.2A, the line has an equal probability of going up or down. Therefore its position at any point will be dependent largely on the sum of all previous events, but will also contain a pure chance element - that of the random number generated in that time step.

A random walk can be applied to studies of evolutionary processes. The vertical axis in Figure 4.2B, for example, represents the form of some morphological trait in an organism; in this case the walk represents the evolution of that trait over time. Bookstein (1987) discussed the application of random walks to evolutionary series, and concluded that it is likely that many trends which are interpreted as stasis, anagenesis, punctuation and gradualism can't be distinguished from elements of a random process.

For this analysis a random walk is taken to represent the changing diversity level of a group of lineages through time, for which a more appropriate form of the Markov chain is a modified branching process. In this model an element can give rise to other elements, with which it then co-exists, or it can cease to exist itself. The branching and extinction process is random, but the number of elements in existence at any one time is strongly influenced by the number that have existed in the preceding time steps. This type of Markov chain is analogous to the origination and extinction of evolutionary lineages using the "budding" model of speciation (Mayr 1963; Eldredge and Gould 1972) where a single ancestral lineage may give rise to multiple descendents.

Random walks generated in this way can be compared with real patterns of lineage diversification as an indication of the extent to which random processes have governed the diversification of life. Only after the stochastic model has been ruled out as a cause for any biodiversification pattern can we start to look for deterministic explanations. In applying the model of a random walk to the evolutionary process we are not saying that individual origination and extinction events are without deterministic cause. Any one event has a complex origin based in genetics, morphology, ecology and

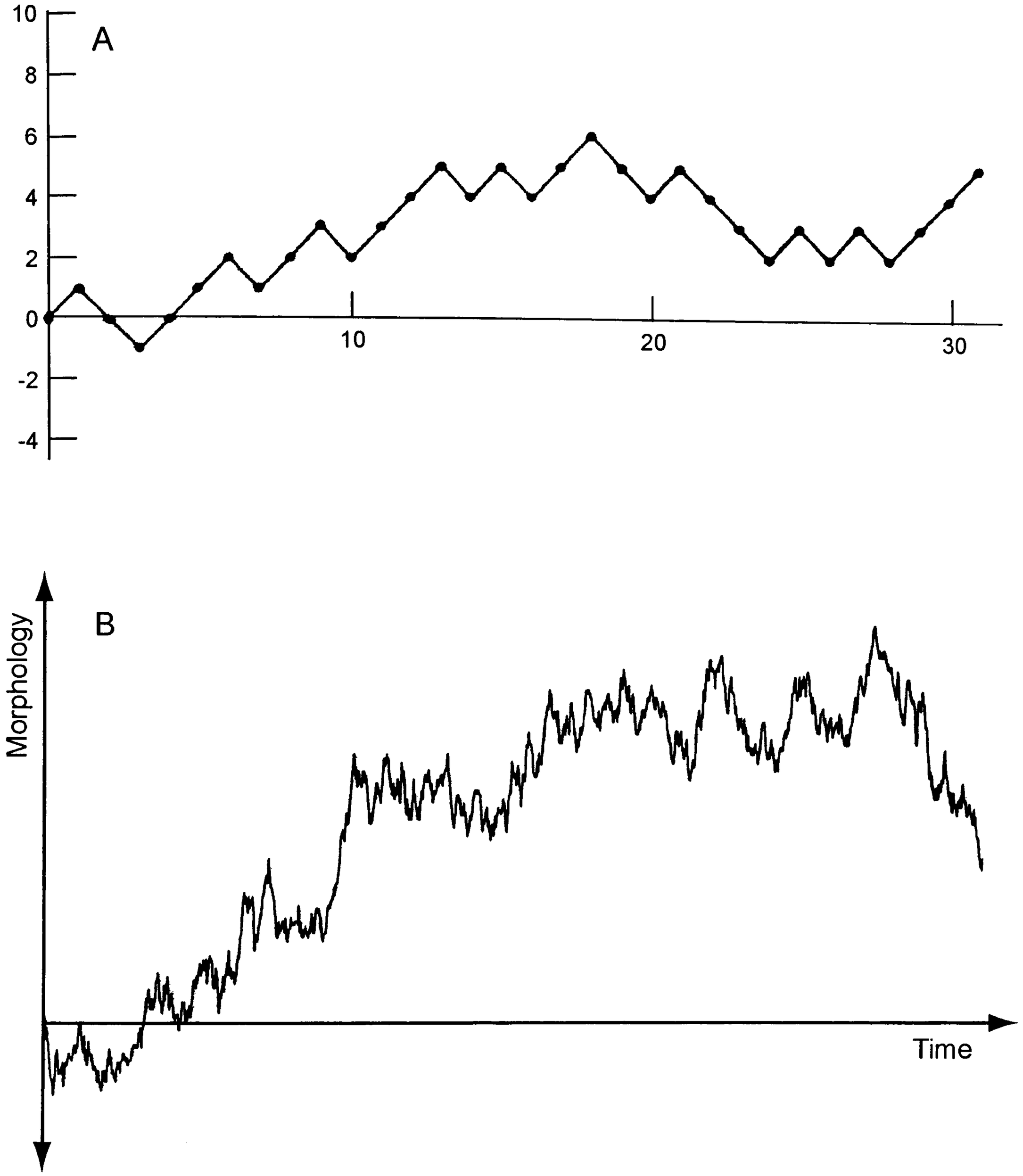


Figure 4.2. Examples of computer-generated random walks. (A) A classic random walk of 31 time steps. With each increment along the x axis the line has an equal probability of going up as down (after Raup 1977 Fig.1). (B) A random walk representing 20 000 tosses of a coin, only every 10th step is drawn. In this case the walk is simulating the evolution of some morphological feature of an organism (after Bookstein 1987, Fig. 1).

biogeography. Taken as a whole, however, the general distribution of extinctions and originations may be quite random (Raup et al. 1973).

In this analysis a random walk simulation is used to test the hypothesis that a long-term stasis in diversity level, such as that seen through much of the Palaeozoic, can arise from a stochastic system without the requirement of deterministic controlling factors.

4.2.2. The CLOCKBACK program

4.2.2.1. Rationale and overview

A new Markovian branching 'random walk' simulation, named CLOCKBACK, is here used to generate evolutionary trees using origination and extinction probabilities calculated from real fossil record data, combined with random number generation. The program was written by Paul Pearson of the University of Bristol, in the programming language Qbasic for the Macintosh, and is here re-written and modified in C for the IBM PC. The program is contained on the IBM disc accompanying this thesis, see Appendix I for source code and Appendix II for IBM disc contents description and program user instructions. This program differs from previous random walk models in several respects. Firstly, taxa newly generated within a time step are cycled through the program and have the potential to either go extinct, or generate offspring of their own within that same time step. These next generation offspring are then in turn cycled, and so on. Not until all taxa, old and new, have been given the opportunity to generate evolutionary events will the program move onto the next time step. In this way a cumulative effect is possible within one time step, and no artificial minimum length of existence is imposed before a taxon can produce an 'evolutionary event'.

Secondly, unlike previous equilibrium models testing the stochastic diversification of clades (e.g. Raup et al. 1973; Gould et al. 1977), there is no control over the topology of the simulated diversity curve in the form of diversity damping to achieve stasis (Fig. 4.3A). Nor are artificial perturbations built into the system to mimic mass extinctions and diversity radiations, as with Hoffman and Fenster's (1986) simulations (Fig. 4.3B). In this respect CLOCKBACK is more similar to the 'freely floating' diversification model of Gould et al. (1977) in which there are no diversity optima, and origination and extinction are equal and unchanging throughout the

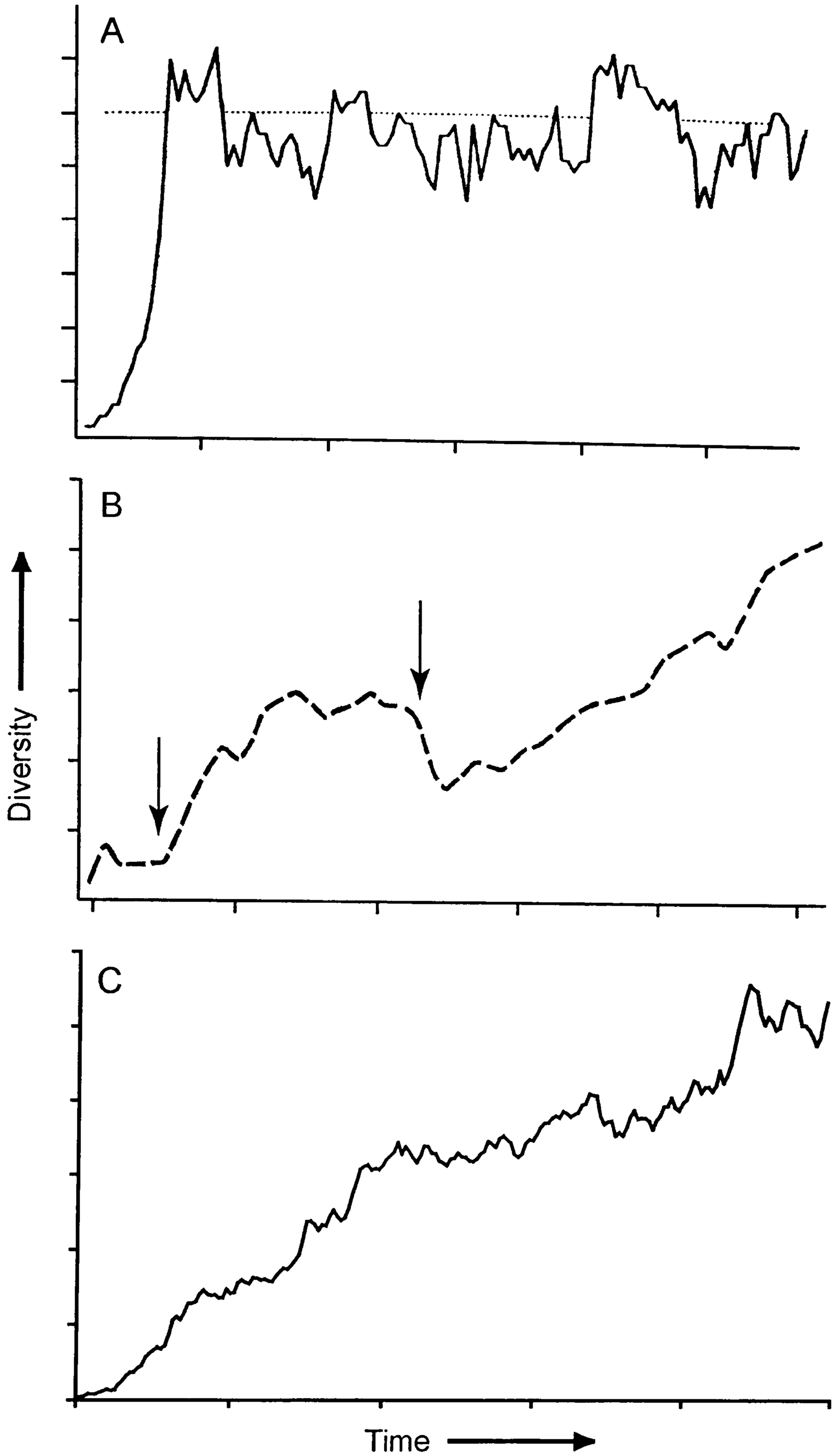


Figure 4.3. Stochastic simulations of biodiversity patterns. (A) The equilibrium model of Raup et al. (1973) uses unequal origination and extinction probabilities combined with diversity damping to produce stasis at a predetermined diversity level, shown by dashed line (after Raup et al. 1973, Fig. 4). (B) Hoffman and Fenster's (1986) simulation uses origination probabilities that are equal and unchanging, but artificial perturbations (indicated by arrows) are built into the system to create mass origination and extinction events (after Hoffman and Fenster 1986, Fig. 4). (C) A typical diversity curve produced by a CLOCKBACK simulation. Origination and extinction probabilities are equal and unchanging throughout the program run, and there are no artificial perturbations.

simulation. CLOCKBACK goes one stage further by having only one input parameter termed the 'evolutionary event probability' which is used to determine both speciation and extinction events. This simplification of the model, and reduction of the number of input parameters, enhances the stochastic nature of the simulation (Fig. 4.3C).

Finally, the program differs from previous theoretical work on evolutionary random walks in the use of an evolutionary event probability calculated from real data, rather than using an arbitrary rate such as the 0.5 events per taxon per time step analogous to coin flipping (e.g. Bookstein 1987). The evolutionary event probability can be calculated from fossil range data of the clade under investigation. Hence the randomly generated diversity curves can be directly compared with the empirical pattern.

The program starts with a single taxon, at time zero, and runs through a series of time steps until it reaches a predetermined endpoint. Within each time step, every extant taxon has the opportunity to generate an evolutionary event – either an origination event (the production of an offspring taxon), or an extinction event (its own extinction), or the taxon can pass through the time step without any effect. Any newly generated taxon also has the opportunity to generate an evolutionary event in turn within the time step. Once all taxa have been cycled in this way, the program moves onto the next time increment. The range information of each taxon is recorded and output once a successful tree is generated. This information is then input to a new version of McGowan's ADAPTS diversity description program (McGowan and Pearson 1999) in order to calculate diversity per time step. This program has been rewritten in C for the IBM PC and is contained on the IBM disc accompanying this thesis. See Appendix I for source code and Appendix II for IBM disc contents description and program user instructions.

The probability of a taxon generating an 'evolutionary event' is determined by the evolutionary event rate, calculated from taxonomic occurrence data of the fossil group under analysis. The evolutionary event rate is calculated by taking the average of the mean per-taxon origination and extinction rates for the group in question over the particular time period of interest. The aim of this analysis is to produce evolutionary trees simulating the familial diversity of all marine life through the latest Precambrian and Phanerozoic. Therefore the per-family rates of origination and extinction for all marine metazoan life through the Phanerozoic were calculated using data from the *Fossil Record 2* (Benton 1993), and averaged to produce the evolutionary event rate

input to the program. Individual event occurrence is determined by comparison of this evolutionary event rate with random numbers generated by the program. Therefore the resulting patterns are stochastic.

A tree is unsuccessful if all its constituent taxa become extinct before the time series reaches the predetermined length input by the user. In addition the modified version of CLOCKBACK allows a minimum value to be set for two defining variables. These variables are tree size (total number of taxa generated) and tree end diversity (number of taxa extant at the end of the time period). If these minimum values are not achieved, the tree is deemed unsuccessful and rejected. This rejection occurs even if the tree reaches the end of the time period with extant taxa. This is to allow greater comparability of the simulated trees with the real clade under investigation, but it obviously leads to a greater number of rejected trees. A further modification within the C version of CLOCKBACK allows specification of the number of successful trees to be generated before the program ceases to run.

4.2.2.2. Parameters and options

The following parameters and program options must be entered for each run:

- Number of successful trees required: the program will run until this number of successful trees has been generated
- Time length of tree: the number of time steps (each representing 1 million years of time) for the program to run.
- Evolutionary rate: this rate determines the probability of an evolutionary event occurring.
- Minimum tree size: the minimum number of taxa required to be generated for the tree to be successful.
- Minimum end diversity: the minimum number of extant taxa required at the end of the program run for the tree to be successful.

Once these parameters have been entered, the program will run until the required number of successful trees has been generated and a results file is output for each.

4.2.2.3. Algorithms

Tree creation

The program starts at time step zero with one taxon. Within each subsequent time step each extant taxon has the opportunity to generate evolutionary events, firstly an origination event and secondly an extinction event. The model of speciation used in the CLOCKBACK program is that of budding: only one daughter taxon is produced by an origination event and the parent does not automatically become extinct as a result (Fig. 4.4). This is the most likely branching pattern predicted by both Mayr's (1974) 'peripatric', or peripheral isolate model and Eldredge and Gould's (1972) punctuated equilibrium model of speciation. It can also be encompassed in models of gradual evolution and sympatric speciation (e.g. Pearson et al. 1997).

Individual event occurrence is determined by comparison of the evolutionary event rate with a random number generated using a member of the RanRot family of pseudo-random number generators, developed by Agner Fog (http://www.agner.org). This random number generator has a virtually infinite cycle length making it especially useful for CLOCKBACK, which, if a large tree size requirement is combined with a low evolutionary rate, can call for millions of attempts to produce a "successful" tree; i.e. a tree of comparable size to the real one under investigation.

For each taxon, within each time step of a program run, two random numbers are generated and compared with the input evolutionary rate. If the first number generated is lower than the rate, an origination event occurs. If the second number generated is lower than the rate, an extinction event occurs. Otherwise nothing happens, and the program moves on to the next taxon.

Within each time step all extant taxa are given the opportunity to generate evolutionary events, including taxa newly created within this step.

Results output

Five pieces of information are recorded about each taxon – an identification number; the time step in which it originated; the time step in which it became extinct; its range in time; and the identification number of its parent taxon. The shortest time range through which a CLOCKBACK generated taxon can persist is one time step, i.e., even if a taxon originates and goes extinct within the same interval, it is still regarded as having a range of one time step.

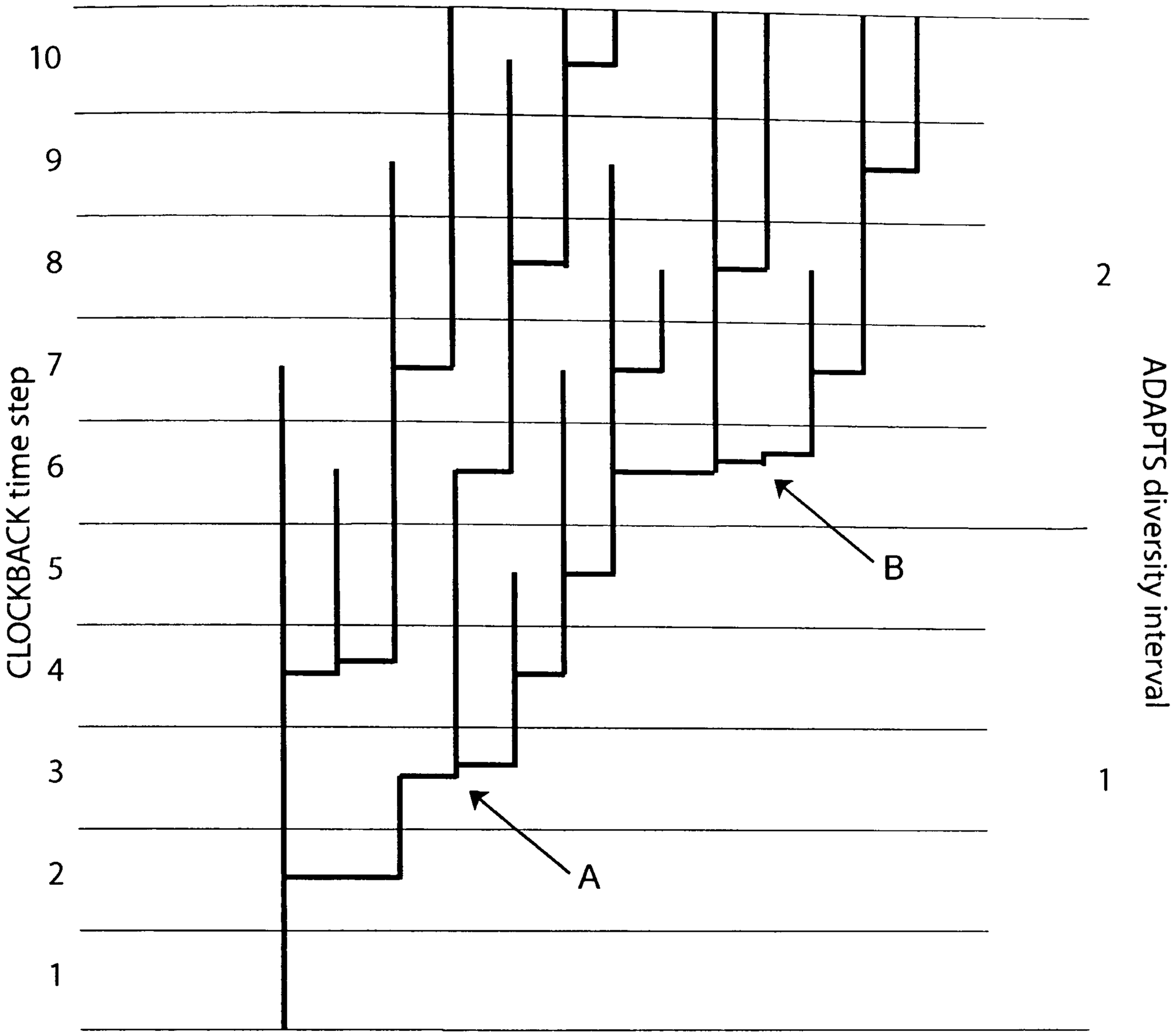


FIGURE 4.4. The CLOCKBACK program budding method of tree growth. Within each time step every extant taxon has the opportunity to first produce an origination event and subsequently an extinction event. This includes taxa newly created within the time step, e.g. branching event A. It can also lead to taxa originating, producing a daughter taxon, and going extinct, all within one time step, e.g. branching event B. Such a taxon is given a time range of one time step. The ADAPTS program is set to have a calculation interval of five CLOCKBACK time steps. Diversity is calculated using the method of Wei and Kennett (1986), where each taxon is weighted according to what proportion of the five time steps it is present in.

This information is output to a results file, which is then input to the ADAPTS program to generate diversity through time data. ADAPTS uses the Wei and Kennett (1986) method of calculating diversity by weighting each taxon by the proportion of a stipulated time interval through which it persists, e.g. a taxon that is present for the whole interval will contribute 1 to diversity, while a taxon only present for half the interval will only contribute 0.5. This method eliminates the problem of diversity counts being related to interval length. For the analysis of the CLOCKBACK data the diversity calculation time interval in ADAPTS was set to five time steps. Therefore a taxon with a range of one time step will contribute 0.2 to the diversity count of one ADAPTS interval (Fig. 4.4).

Three additional pieces of information are output for each successful tree: the number of unsuccessful attempts required to generate the tree, the tree size (total number of taxa) and the number of extant taxa.

Unsuccessful trees

If a tree is unsuccessful, i.e. becomes extinct or does not fulfil the minimum tree size or extant taxa requirements, the program re-starts from a single taxon at time zero and begins another attempt.

4.2.3. Parameters used

The aim of this analysis has been to produce 100 successful trees using the following parameters:

- Time length of tree: 1000 time steps. This represents 1000 million years of evolutionary time.
- Evolutionary rate: 0.023 events per taxon per time step (million years). This is the average of the mean per-family origination (0.027) and extinction (0.019) rates for Phanerozoic marine life, as calculated from *Fossil Record 2* (Benton 1993) data.
- Minimum tree size: 3500 taxa. The Precambrian and Phanerozoic marine fossil record contains approximately 3900 families.
- Minimum end diversity: this was set at 1 taxon for this analysis, i.e. provided the tree has at least 1 extant taxon at the end of the run it is deemed successful if the

total number of taxa within the tree exceeds 3500. For this study it was considered more important that the total number of taxa should be comparable to that of marine fossil families rather than the number of extant taxa should equal that of the present day.

4.2.4. Criteria for identifying a "plateau" period

The diversity histories of the 100 successful trees were scrutinized to determine which include diversity patterns that resemble the diversity stasis period of the Palaeozoic marine family curve. The following criteria were used to define a "plateau time period":

1. **Minimum time period length: 200 time steps.** The Palaeozoic plateau diversity stasis period runs from the Caradoc to the Kungurian, approximately 200 myr.
2. **Mean per taxon rate of diversification (r_d) over plateau period: – 0.0003 <= r_d <= 0.0003.** For a perfect 'plateau period' the mean rate of diversification (r_d) would equal 0. For this search the upper and lower limits of mean r_d were defined by the mean r_d of the Palaeozoic plateau period, which equals 0.0003 as calculated from *Fossil Record 2* data (Benton 1993). For definition of r_d see Chapter 1, Section 1.2.1.
3. **Standard deviation of diversity: <= 6.3% of mean diversity.** Standard deviation as a percentage of mean diversity is used to limit the fluctuations in diversity allowed around the 'plateau' level. Standard deviation is expressed as a percentage of diversity, rather than an absolute value. This means that greater fluctuations are allowed at higher diversity levels than at lower levels. During the Palaeozoic diversity stasis period the standard deviation of diversity equals 6.3% of mean diversity level.

To identify plateau periods, successive 200 myr. intervals of the diversity history of each tree were searched in order to establish if they fulfilled criteria 2 and 3 above.

Curve fitting

As a final test for diversity stasis periods, a least-squares fit of Sepkoski's (1978) logistic diversification model (Chapter 1, Equation 1.12) was applied to each of the diversity curves that include a time period fulfilling the plateau criteria above. The D_0

parameter of the model (initial diversity) was constrained to equal 1, as each tree commences with one taxon. For those curves with 'plateau' periods ending at more than 100 time steps before the end of the tree, a fit of the model was only applied to up to the end of the plateau period.

4.3. Results

Unsuccessful trees

More than 2×10^9 unsuccessful trees were generated in the course of producing 100 successful trees. This large number of failed trees is a consequence of the parameters input to the program to define a successful tree (see section 4.2.3), i.e. a high tree size (3500 taxa) combined with a low evolutionary event rate (0.023 events per taxon per million years). This success to failure ratio of approximately one to 20 million demonstrates the very small probability that the diversity pattern evident in the Phanerozoic fossil record arose by chance, with origination events having no greater probability of occurring than extinction events throughout the time period (but see discussion, Section 4.4. below).

Successful trees

Sixty-nine out of the 100 successful trees display diversity histories that fit 'plateau' defining criteria outlined above (Section 4.2.4). Figure 4.5 illustrates diversity curves of typical examples of successful trees with identified plateau periods (shown in bold). Some of these plateau periods are of a time length considerably longer than the minimum of 200 time steps, e.g. Figure 4.5A, G and O. The least-squares fit of Sekoski's logistic model (Sepkoski 1978) is shown along with the R^2 value for the fit. The complete set of sixty-nine diversity curves for successful trees containing plateau periods is illustrated in Appendix III.

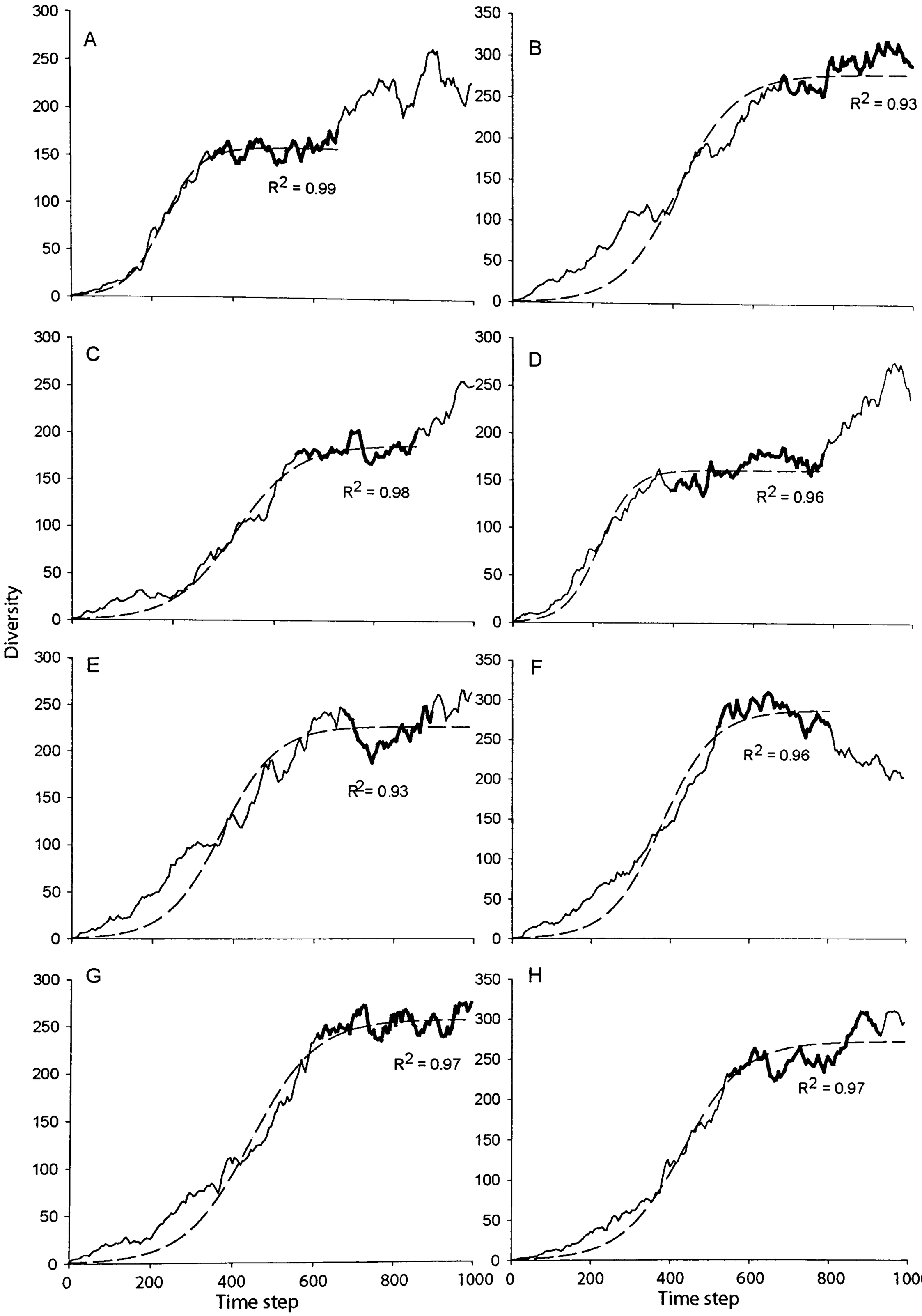
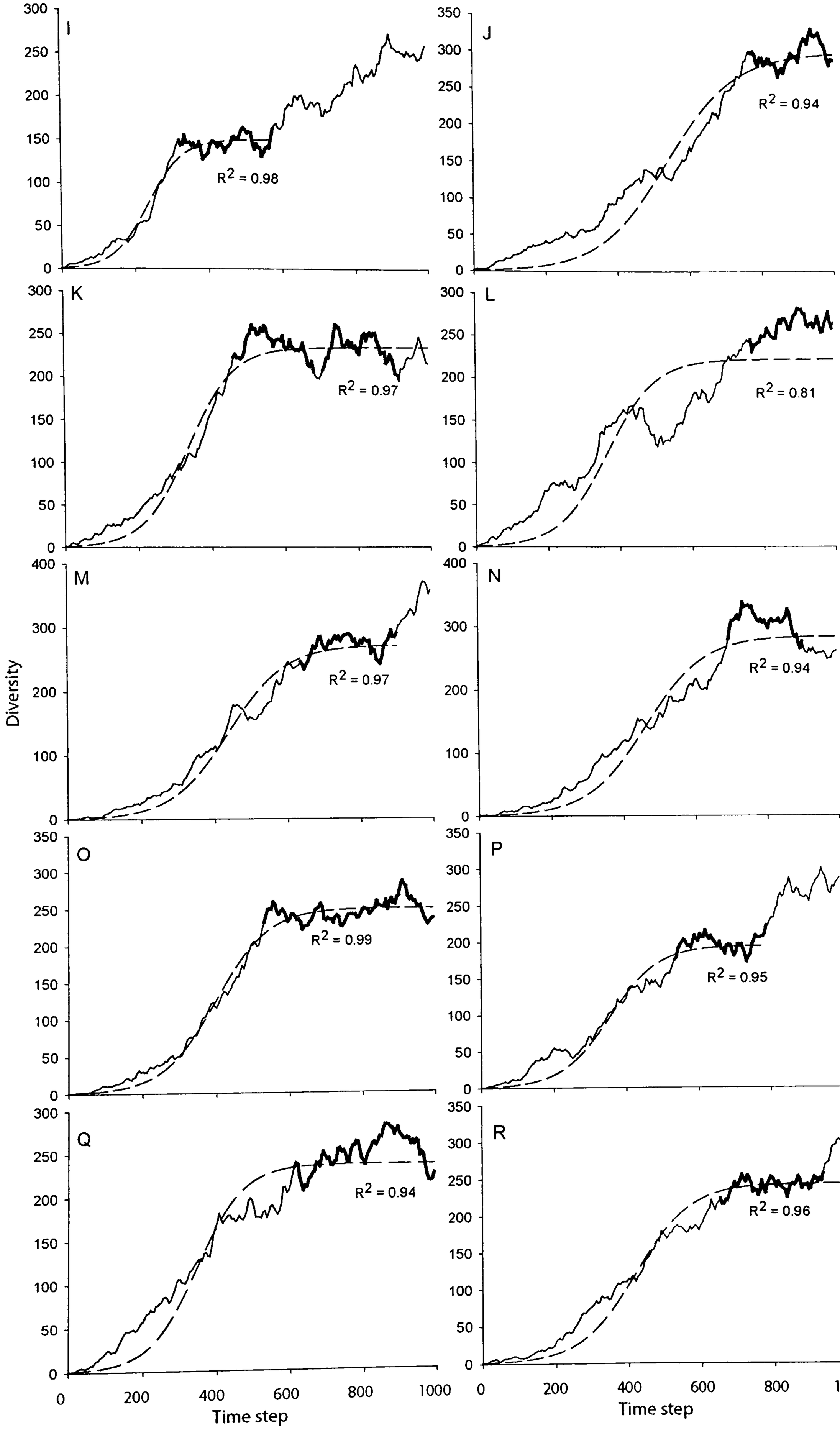


FIGURE 4.5. Example CLOCKBACK program runs containing 'plateau periods': time periods where the diversity pattern meets plateau criteria. (A-R) Diversity is measured using the method of Wei and Kennett (1986). Sections of the diversity curve meeting the plateau defining criteria are shown in bold. Each curve has a least-squares fit of the logistic model of Sepkoski (1978), with initial diversity constrained to equal 1 lineage. For curves with 'plateau' periods ending at more than 100 time steps before the completion of the curve, the model has only been fit up to the end of the plateau period. The correlation coefficient for each fit is given.


I
$R^2 = 0.98$
J
$R^2 = 0.94$
K
$R^2 = 0.97$
L
$R^2 = 0.81$
M
$R^2 = 0.97$
N
$R^2 = 0.94$
O
$R^2 = 0.99$
P
$R^2 = 0.95$
Q
$R^2 = 0.94$
R
$R^2 = 0.96$
Diversity
Time step
Time step

Fit of logistic model

In all sixty-nine cases the least-squares fit of the logistic model to the tree diversity history is good: R^2 values range from 0.81 to 0.99 with a mean of 0.96. In the majority of cases the flattening out of the logistic model corresponds to the purported plateau period of the CLOCKBACK generated diversity curve (an exception is Fig. 4.5L, which has the lowest R^2 value). This combined with the high R^2 values, indicates that the logistic model is a good description of these diversity histories, even though the curves were produced by stochastic rather than logistic processes.

Two observations can be made on the basis of a visual examination of the complete set of results curves. Firstly many of the plateau periods occur at the end of the diversity curves. Only a few (e.g. Fig. 4.5A, C and D) contain plateau periods before or at the midpoint of the curve, followed by a further rise in diversity level. The reason for this is explained in Figure 4.6. The system is constrained to reach a total diversity level of 3500 taxa in 1000 time steps, simulating the situation during the Phanerozoic. If a plateau period occurs early in the evolution of the system it must come after a very rapid initial diversification period - otherwise there is insufficient time after the plateau has ended for the required level of total diversity to be reached. Such a very rapid initial diversification is unlikely in a purely stochastic system. Only six of the 100 successful trees contain a plateau period with an origin at less that 500 time steps into the program run. This indicates that any stasis period is more likely to occur at the end than near the beginning of a system operating under the diversity and time constraints of the Phanerozoic fossil record

Secondly some of the examples shown in Figure 4.5 contain time periods meeting the plateau criteria, although they do not resemble a plateau visually. In particular, periods of an initial rise in diversity followed by an equal fall (i.e. a 'hump' shaped curve), often fit the criteria as their mean per taxon rate of diversification averages to zero, and the standard deviation does not exceed the limits of the diversity mean stipulated, e.g. Figure 4.5F, N and Q. The same is true for 'plateaux' which are actually dips in diversity e.g. Figure 4.5E. These intervals that meet the plateau criteria, despite not having the appearance of equilibria, are discussed in the following section.

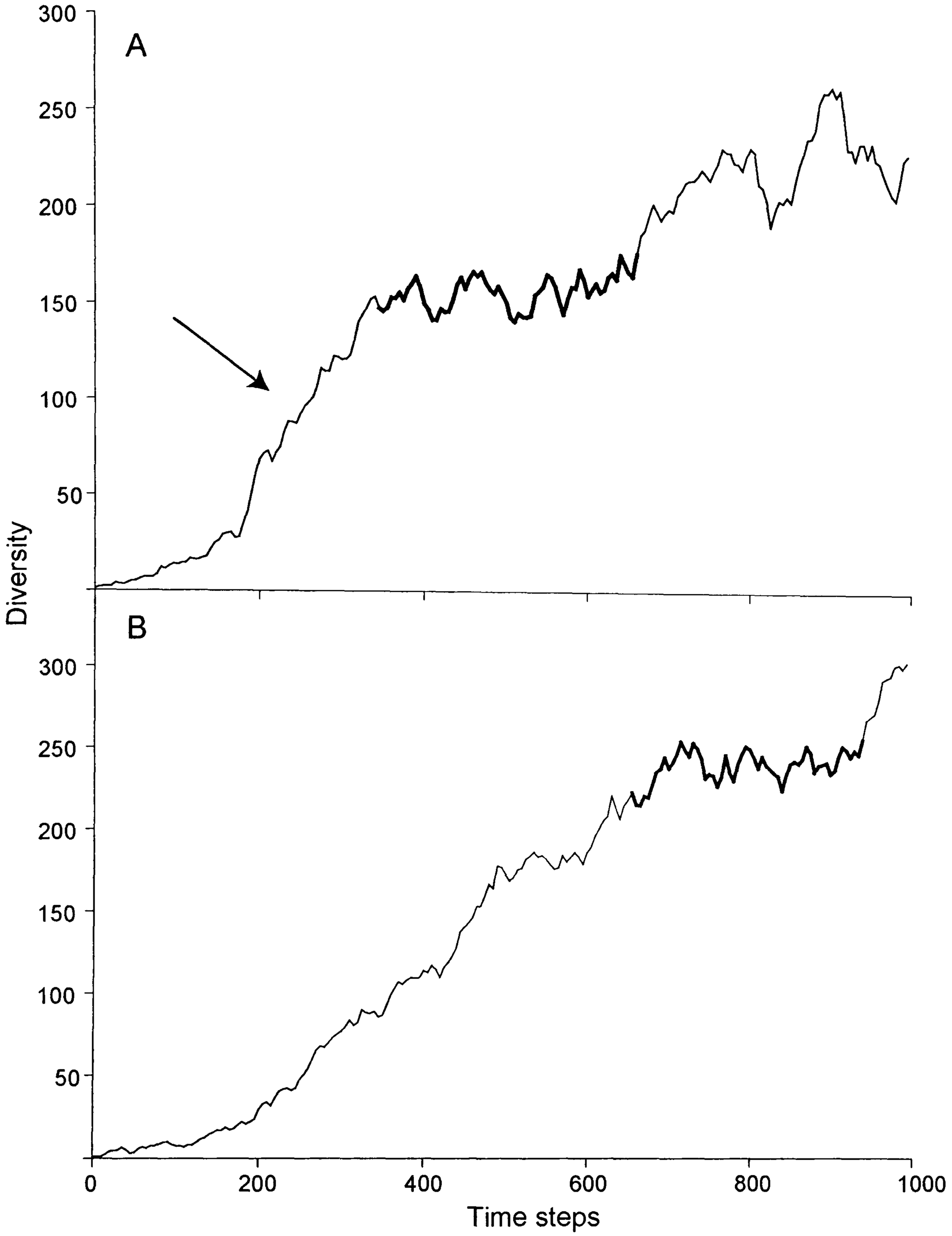


Figure 4.6. Stasis periods occur late in the diversity curves. (A) An example of one of the six CLOCKBACK curves out of 100 containing a plateau period (bold line) with an origin less than 500 time steps into the program run. For this tree to reach the required total number of taxa (proportional to total area under the curve), there must be a very rapid initial period of diversification (indicated by arrow). Such a rapid rise is unlikely to happen in a purely stochastic system. (B) A more typical CLOCKBACK run with the stasis period occurring late in the curve. A less explosive rise in diversity up to the stasis level is required.

4.4. Discussion

The very small number of successful trees compared to the vast number of unsuccessful trees rejected by the program demonstrates the improbability that anything approaching the level of diversity evident in the fossil record arose by chance in the time available for evolution. Therefore there must have been a greater propensity for taxa to originate during the Phanerozoic than to go extinct. A stochastic simulation of diversification where the probability of origination exceeds that of extinction always produces a exponential growth curve. The only way to produce a stasis period in such a system is to implement some kind of diversity damping mechanism (e.g. Raup et al. 1973).

A group of ideas that have grown out of cosmology and theoretical physics, collectively named the 'weak anthropic principle' (Barrow and Tipler 1986), limits acceptable cosmological and evolutionary theories to those that allow for the certainty of life and human evolution. This principle is summarised by the statement: "What we can expect to observe must be restricted by the conditions necessary for our presence as observers" (Carter 1974, p. 291). According to the anthropic principle, when considering how nature might have evolved otherwise, we need not calculate the odds against the infinity of all other possibilities, but only against those that permit the emergence of life and of ourselves as observers. In the context of this study it could be argued that any random pattern of diversification that does not reach a substantial diversity level can be rejected immediately as of no consequence and can be excluded from any probability analysis.

Whether or not we accept this philosophical constraint (and Gould [1983] did not), the question posed by this analysis is not 'what is the probability that the level of diversity we see in the fossil record has arisen by chance?' but rather 'if we accept the fossil record diversity level as given, what is the probability that, by chance, a long term diversity stasis period will be seen as part of its pattern of diversification?'. The results suggest a 69% chance of such a stasis period arising. Examination of the examples in Figure 4.5 demonstrates that a diversity stasis period is not unlikely to have arisen randomly. Indeed all the other major features of the Phanerozoic marine curve can also be identified – periods of unfettered origination, extinction events (both sudden and gradual), diversity peaks and troughs – although a mass extinction on the scale of the end-Permian or K-T event is not evident and is an unlikely feature to be produced stochastically. Bookstein (1987) implied that long term diversity equilibria are outside

the null model of a random walk. Here, however, it has been shown that, if certain constraints regarding level of diversity and length of time are accepted, a period of diversity stasis is highly probable in a stochastic evolutionary tree with an evolutionary event rate similar to that of marine life through the Phanerozoic.

Such a diversity plateau is most likely to occur at or near the end of the diversity curve. A stasis period early in the evolutionary history of the Phanerozoic proves to be less probable, with the required 'Cambro-Ordovician'-like explosion of taxa at the beginning of the curve, followed by a plateau, only occurring in 6% of successful trees. It is therefore proposed that the null model of stochastic diversification on its own is not sufficient to explain the diversity dynamics of marine life through the Palaeozoic. Certainly a diversity rise such as that seen in the Ordovician is an improbable feature of a purely random walk, and the evidence supports a higher origination than extinction rate during this period, deterministically produced by one or more ecological and biological factors. It is possible that there was a switch from deterministic to stochastic processes subsequent to the Ordovician rise, and the Palaeozoic plateau is a feature of random processes rather than ecological constraints. Hoffman and Fenster (1986) demonstrated that a model of predominately stochastic evolution, with input of extra taxa to produce the Ordovician rise, can reproduce the Palaeozoic diversity curve with some accuracy (see Fig. 4.3B). However, without further evidence, it is difficult to determine whether the switch from origination rate-driven diversification in the Ordovician, to equal origination and extinction probabilities in the Silurian-Permian was a product of stochastic or deterministic processes.

Further criteria defining a 'plateau period' may be needed to reduce the number of purported plateaux found. Some of the identified 'plateaux' in the simulations are a product of diversity 'humps' and 'troughs'. This highlights a problem with the purported empirical multiple equilibria seen in the marine diversity pattern. The actual period of the Palaeozoic plateau fits only a small number of defining criteria, those of a low mean rate of diversification, and a good fit to Sepkoski's logistic diversification model. These alone are not sufficient to prove diversity-dependent dynamics or the existence of an ecologically controlled period of stasis (Sepkoski 1978). Further tests are required.

The apparent ease with which equilibrium periods can be produced in a stochastic system should not be interpreted as evidence against the existence of some over-arching deterministic ecological or biological constraints during the Phanerozoic.

Indeed Kitchell and Carr (1985) warned against using pattern alone to imply either randomness or order within a system, as determinism may yield chaos, and randomness may yield order. The evolutionary event rate used in these simulations was calculated from fossil data, and may have been determined by large-scale ecological factors. It could therefore be argued that determinism has been built into the stochastic system. Evidence beyond the shape of the Phanerozoic marine diversity curve, and the good fit of the logistic model, is required before deterministic controls such as large scale diversity damping caused by inter-clade competition can be accepted.

4.5. Conclusions

- Stochastically generated simulations suggest that the level of taxonomic diversity seen in the fossil record is extremely unlikely to have arisen by chance if speciation and extinction rates have always been equal.
- If this is the case it is likely that there was a greater propensity for taxa to originate rather than to go extinct over the course of the Phanerozoic. Such a predisposition towards origination always produces an exponential growth pattern unless a diversity damping mechanism occurs, i.e. an increase in extinction or a decrease in origination rate. This is true even if speciation rate is only slightly higher than extinction.
- If the fossil record diversity level is accepted as given, there is a probability in the region of 70% that a prolonged period of diversity stasis will have occurred by random processes at some point during the diversification of marine life.
- Such a stasis period is more likely to occur towards the end of the diversity curve for a system with diversity and time constraints matching those of marine life through the Phanerozoic.
- Therefore, while the null model of stochastic diversification for the general equilibrium theory is not rejected, it is unlikely that the Palaeozoic plateau is a purely stochastic structure. A combination of deterministic expansion in the Ordovician followed by stochastic stasis through the Silurian-Permian may be more likely. Further investigation of the exact nature of originations and extinctions through the Palaeozoic is required.

- Many of the other features of the Phanerozoic diversity pattern can be created by stochastic processes, e.g. periods of apparent unfettered origination, and mass and gradual extinctions.
- The fulfilling of the plateau criteria by some of the stochastic curves that do not look like stasis periods demonstrates the need for more rigorous tests of diversity equilibria, e.g. demonstration of diversity dependence in underlying rates.

CHAPTER 5. THE PALAEOZOIC PLATEAU – AN ECOLOGIC STRUCTURE?

5.1. Introduction

If the Palaeozoic plateau structure seen in the familial and generic marine diversity curves is real, and not an artefact of taxonomy, what is its biological significance? Sepkoski (1981; Sepkoski and Miller 1985; see also Flessa and Imbrie 1973) in recognising the equilibrium, and proposing the three evolutionary faunas, each with its own logistic diversification pattern, advocated two fundamental macroevolutionary concepts: (1) the notion of a global carrying capacity for the Earth, or at least for the Earth's oceans - a finite number of species sustainable by the biosphere, which has in the past been reached on at least two occasions; (2) the related concept of large scale interclade or even interfaunal competition, with competitive displacement of higher taxa occurring over evolutionary time. From these emerge the theories of diversity-dependent origination and extinction rates.

5.1.1. Global carrying capacities

The apparent stasis in numbers of families and genera through much of the Palaeozoic is seen by proponents of the equilibrium theory of biodiversification to be a result of the slowing and then gradual reduction in diversity levels of the Palaeozoic fauna, combined with (and produced by) the increasing diversity of the Modern fauna (Sepkoski 1979, 1981, 1984). As each fauna increases in taxon number its own diversity level will be progressively more affected by the growth of the next, so producing a diversity-damping effect and the resulting equilibrium level. The slowing and eventual halt of diversification suggests a global carrying capacity, i.e. a limit to the numbers of species and higher taxa that can be sustained by the Earth's resources.

Whittaker (1977) insisted that the Earth's biosphere has always been far removed from any theoretical carrying capacity, and argued that the appearance of new species actually creates new resources and hence new ecological opportunities for further diversification. Such co-evolution, the evolutionary niche of one species being created, defined and affected by the evolution of another, is one of the major processes organizing the Earth's biodiversity (Thompson and Cunningham 2002). The biosphere may also have been kept far below any carrying capacity by physical events and

perturbations that do not allow an equilibrium diversity to be reached (Hoffman 1989) although, if such perturbations are randomly distributed through time, it could be argued that they are one of the defining parameters of a global carrying capacity. Benton (1997, 2000) also rejected the global carrying capacity theory, suggesting that species innovation, or the evolutionary tendency of species to 'find new things to do' will prevent the establishment of long-term diversity equilibria. A pre-ordained, absolute upper-bound on diversity was seen as an inherent problem of the logistic model by Kitchell and Carr (1985). They rejected this assumption and instead proposed a model of diversification where any limit was dependent upon historical events of evolution, and included the potential for evolutionary innovation, i.e. new species with novel adaptations entering the system and thereby 'relaxing' the upper bounds on diversity.

Kirchner and Weil (2000b), in a study of Phanerozoic evolutionary rates based on Sepkoski's (1992, unpub.) data sets, found that both raw and de-trended origination rate time series display stronger autocorrelation (self-correlation) than extinction rate time series over lag times of 5 to 30 million years. Extinction rates display no stronger autocorrelation than that which could be expected to have arisen by chance. Two biological reasons were given for these results: (1) each new species represents a potential evolutionary starting point for new originations, key innovations result in adaptive shifts that allow subsequent radiations; and (2) new taxa themselves constitute new niches, for predators, parasites and symbionts. Therefore, origination events seed new originations and hence radiations, trends which scale up over increasingly longer time scales. Kirchner and Weil (2000b) concluded that the primary mechanism driving diversification events through the Phanerozoic is the creation of new evolutionary niches, and new evolutionary pathways for reaching them, by diversification events themselves, rather than by emptying pre-existing niches.

5.1.2. Competitive displacement and diversity-dependent turnover

The mechanism underpinning theories of long-term global carrying capacities is the macroevolutionary competitive displacement model. This is an extension of ecological species-area theories such as that of island biogeography (MacArthur and Wilson 1967) which was later expanded to the scale of continents or other large biogeographic units (Rosenzweig 1975). In numerous experimental situations, both under laboratory conditions (e.g. Gause 1934) and within natural habitats (e.g. Kennedy et al. 2002),

species are shown to compete with one another for existing resources which define a finite number of ecological niches available for exploitation. This process maintains overall diversity within an area at a constant level, with this level being higher the larger is the available amount of habitat (the species-area effect). However, what is not clear is the extent to which such ecological results can be scaled up to geological time-scales and macroevolutionary situations (Benton 1995, 1997, 2000).

Kemp (1999) cited two difficulties with the macroevolutionary competitive displacement theory. The first is the implication that higher taxa can behave as interacting units. There would have to be some characteristic of the taxon as a whole, rather than of the individual species that comprise it, which was the cause of the survival or extinction of the taxon. Failing this, it must be assumed that within the taxon all individual species share characteristics, such that in every case of species-to-species competition the species belonging to the first taxon out-compete the corresponding species in the second, thus causing the replacement of the first taxon as a whole. The second scenario is that favoured by Sepkoski (1996a) who emphasised the term *clade displacement*, a process produced by species competition, rather than *clade competition*. Investigations of inter-species competition on a global macro-evolutionary scale are impossible with currently available data. Regional studies have identified co-"coordinated stasis" (periods of stability punctuated by short periods of high turnover) in detailed analyses of Silurian and Devonian faunas from the Northern Appalachian Basin (Brett and Baird 1995), but rejected it in Middle and Upper Ordovician articulate brachiopod species from a similar geographic area (Patzkowsky and Holland 1997). In such regional studies immigration and emigration of species is as likely an outcome of competition as origination and extinction. Westrop and Adrain (1998) conducted a study of trilobite alpha diversity from the Late Cambrian to the Late Ordovician and concluded that while there was a decline in relative importance of the group, this was achieved not through displacement, but by dilution from newly radiating invertebrate groups. The findings imply that direct competitive interactions between the Cambrian and Palaeozoic faunas were not important in the Ordovician transition from trilobite to articulate brachiopod dominated communities.

The second difficulty (Kemp 1999) with competitive displacement is the time required for one clade to replace another. For the global displacement of a taxon to be evident in the fossil record it would have to have a time span of millions of years, in which case the competitive edge of one taxon over another would be so slight that

chance factors would be expected to play a far more significant role in the outcome than any element of deterministic competition (Benton 1987), unless competition was strong but only intermittent. A possible answer to this is the theory of incumbent replacement (Rosenzweig & McCord 1991) where a clade, whose species occupy a range of niches, can only be replaced gradually by the species of a competing clade as those of the incumbent clade become extinct. This leads to a time scale for replacement of the whole clade which is determined by the extinction rate of its constituent species, a rate that may be very low. Sepkoski (1996a), coupling classic population ecology competition theory with evolutionary change within species, and environmental change within habitats, proposed a number of other scenarios where two competing clades can co-exist for long spans of time, thus allowing identification of competitive interaction and clade displacement in the fossil record.

Empirical evidence for higher taxon, or inter-faunal, competitive displacement over evolutionary time is equivocal (Fig. 5.1). Niklas et al. (1985; Niklas 1986) reviewed the biodiversity of land plants from 420 million years ago until the present, and identified four successive evolutionary faunas. They concluded that the appearance of novel structural or reproductive 'grades' of plants in some cases caused the large scale competitive displacement of older forms, e.g. the angiosperms competing with the gymnosperms for similar habitats (Fig. 5.1A), although this cannot be viewed as a complete replacement as the gymnosperms are still extant today. Maas et al. (1988) also found evidence for displacement over evolutionary time in the extinction of plesiadapiform primate-like mammals from North America. Patterns of taxonomic richness and relative abundance of non-paromomyid pleisiadapoids show an inverse relationship with those of rodents, with which they are thought to have competed for resources (Fig 5.1B).

Conversely, Gould and Calloway (1980) investigated the possibility of competitive displacement of the Palaeozoic dominant brachiopods by the bivalves of the Modern fauna (Fig. 5.1C). They concluded that the competition explanation does not fit the empirical data, and instead considered the diversity histories of both clades to be the product of the end-Permian mass extinction, which differentially affected each group. However, Sepkoski (1996a) reconsidered this case and produced a solution to a pair of coupled logistic equations with parameter values estimated from the two clades in question, which mimic the form of both diversity patterns. This led Sepkoski to

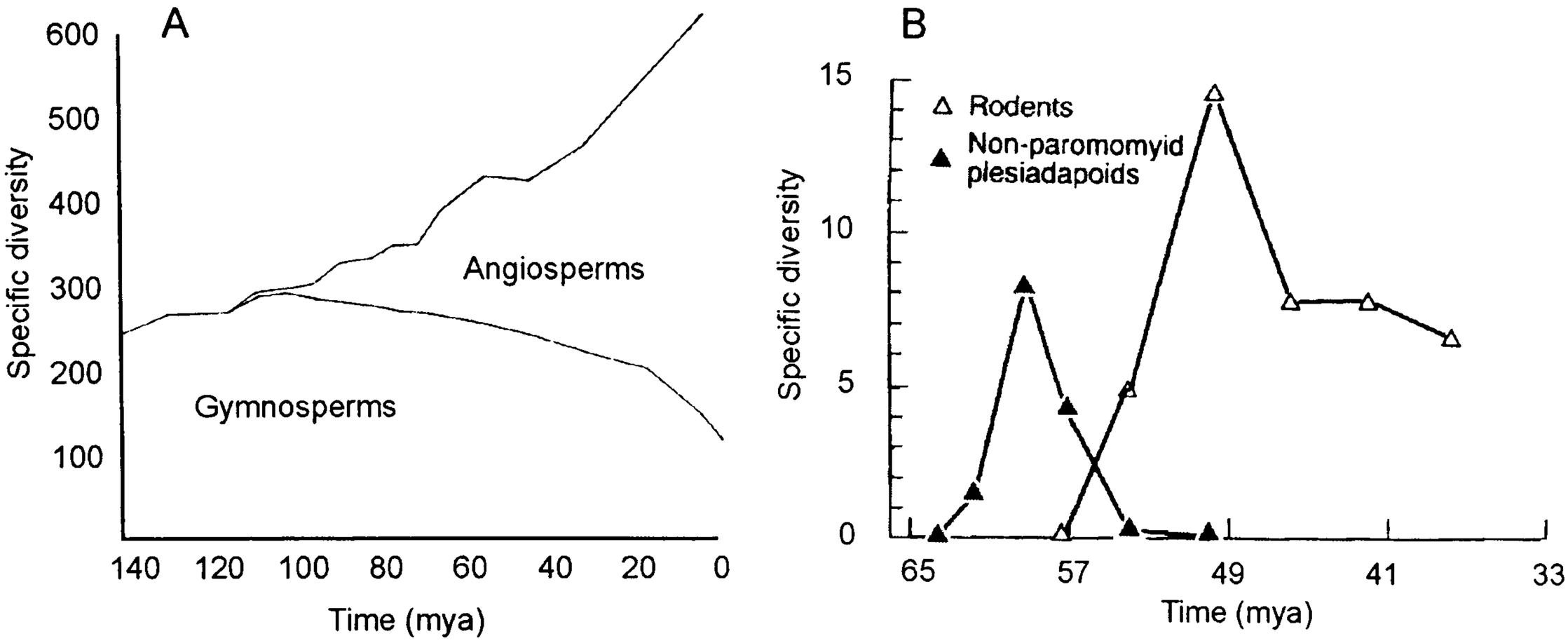


FIGURE 5.1. Examples of diversity curves displaying proposed competitive displacements. The 'winner' in each case is given first (A) Angiosperms vs. gymnosperms (after Niklas et al. 1985). Curves plotted cumulatively. (B) Rodents vs. plesiadapid primates (after Maas et al. 1988). (C) Bivalves vs. articulate brachiopods. Data from Sepkoksi (unpub.). (D) Cheilostome vs. cyclostome bryozoans (after Sepkoski et al. 2000). Curves plotted cumulatively.

conclude that articulate brachiopods may indeed have been displaced by bivalves competitively. Further empirical studies which question the competitive displacement model included those of Lidgard et al. (1993) on cyclostome and cheilostome bryozoans (Fig. 5.1D) (although see Sepkoski et al. (2000) for a model of this interaction using coupled logistic equations) and Smith (1988) on early Palaeozoic echinoderms. Using cladistic analysis at generic level to identify 'ghost ranges' of taxa, Smith found that diversification of Cambrian and Ordovician echinoderms appeared to display a pattern of continuous expansion, and not two phases of radiation followed by competition as previously suggested (Paul 1979). A study by Skelton et al. (1997) of rudist bivalve and coral assemblages from the Santonian carbonate platform deposits of the Spanish Pyrenees, found no evidence of mutual interference between these two groups, and disputed the hypothesis that rudists competitively displaced corals during the Cretaceous. Benton (1985, 1989, 1996) plotted the diversity of terrestrial tetrapod families against time, and while recognising three successive major radiations, he did not find any evidence of inter-faunal or interfamilial competitive displacements between tetrapod groups. In this case it is likely that adaptive expansion is the more significant factor, with the increase in vertebrate diversity being due to their ability to exploit new habitats and utilise new resources (Benton 1990). Benton (1996) also specifically looked for Candidate Competitive Replacements (CCRs) among tetrapod families, a CCR being defined as a family origination that coincides stratigraphically with a family extinction, and where the pair share a similar mode of life and an overlap of geographic ranges. He concluded that the majority of tetrapod originations cannot be considered as putative examples of competitive replacement. Unfortunately marine invertebrate taxa are less accommodating to such a detailed analysis, due to the less specialised mode of life and more diffusely defined geographic ranges of most marine invertebrate life. For example there are nearly two thousand non-singleton bivalve genera known from the fossil record (data from Sepkoski's unpublished generic database), which could be interacting competitively with a similar number of articulate brachiopod genera. Many share overlapping stratigraphic ranges, and modes of life are similar between the epifaunal feeding bivalves and brachiopods (although infaunal bivalves could be excluded from the competition theory [Sepkoski 1996a]), and there is evidence for the spreading of bivalves from near-shore settings out to the brachiopod dominated middle shelf habitats as the Palaeozoic progressed (Miller 1988). With such large numbers of taxa not easily 'pigeon-holed' into small enough categories to test directly for

competitive displacement, a better method of investigating interaction is to document the overall trends of diversity, patterns of originations and extinctions, and taxonomic longevity within and between groups.

Hence, the analysis of fossil taxonomic origination and extinction rates can be used to investigate the reality of inter-cladistic competition within the marine realm. If global equilibria are a reality, the underlying taxonomic turnover rates should display *diversity-dependence*, or the damping of origination rates combined with a raising of extinction rates as the diversity equilibrium level is neared. The rates should equal each other at the point of equilibrium. Sepkoski (1978) recognised that the mere shape of the Phanerozoic diversity curve was not enough to prove the logistic model of diversification, and suggested that evidence of the diversity-dependence of the underlying turnover rates was essential to demonstrate dynamic equilibria. He proceeded to formularise linear and parabolic functions modeling the diversity dependent behaviour of both per-taxon and total rates of origination and extinction with changing standing diversity (See Chapter 1, Section 1.2.1 for mathematical definitions of these rates, and Section 1.3.2.1 for Sepkoski's models). The expected form of the models is given in Figure 1.4, and shown in greater detail in Figure 5.2.

Plots of total ordinal origination and extinction rates (number of events per million years) against standing diversity for Phanerozoic series demonstrate a reasonable fit of the diversity-dependent equations to the origination rate curve, but only a poor fit to extinction rate data (Sepkoski 1978). A similar analysis of familial data for post Mid-Cambrian Palaeozoic series (Sepkoski 1979) found 61% of the origination rate data encompassed by the diversity-dependent model, but only 11% of the extinction rate data, suggesting that origination rates may be diversity-dependent, but that extinction rates are not. Similarly, Alroy (1998) found Cenozoic mammal origination rate data a better fit to a diversity-dependent model than extinction rate data. Conversely, Foote (2000b) came to the opposite conclusion when testing for a correlation between first-difference data of Phanerozoic marine generic diversity and 'per-capita' origination and extinction rates. In his analysis extinction rate was found to have the stronger correlation with diversity during the Palaeozoic, although the situation seems to be reversed in the Post-Palaeozoic. Flessa and Levinton (1975) tested for diversity-dependence during the Phanerozoic by seeking a correlation between family total extinction and origination rates, i.e. testing the hypothesis that the two rates will equal

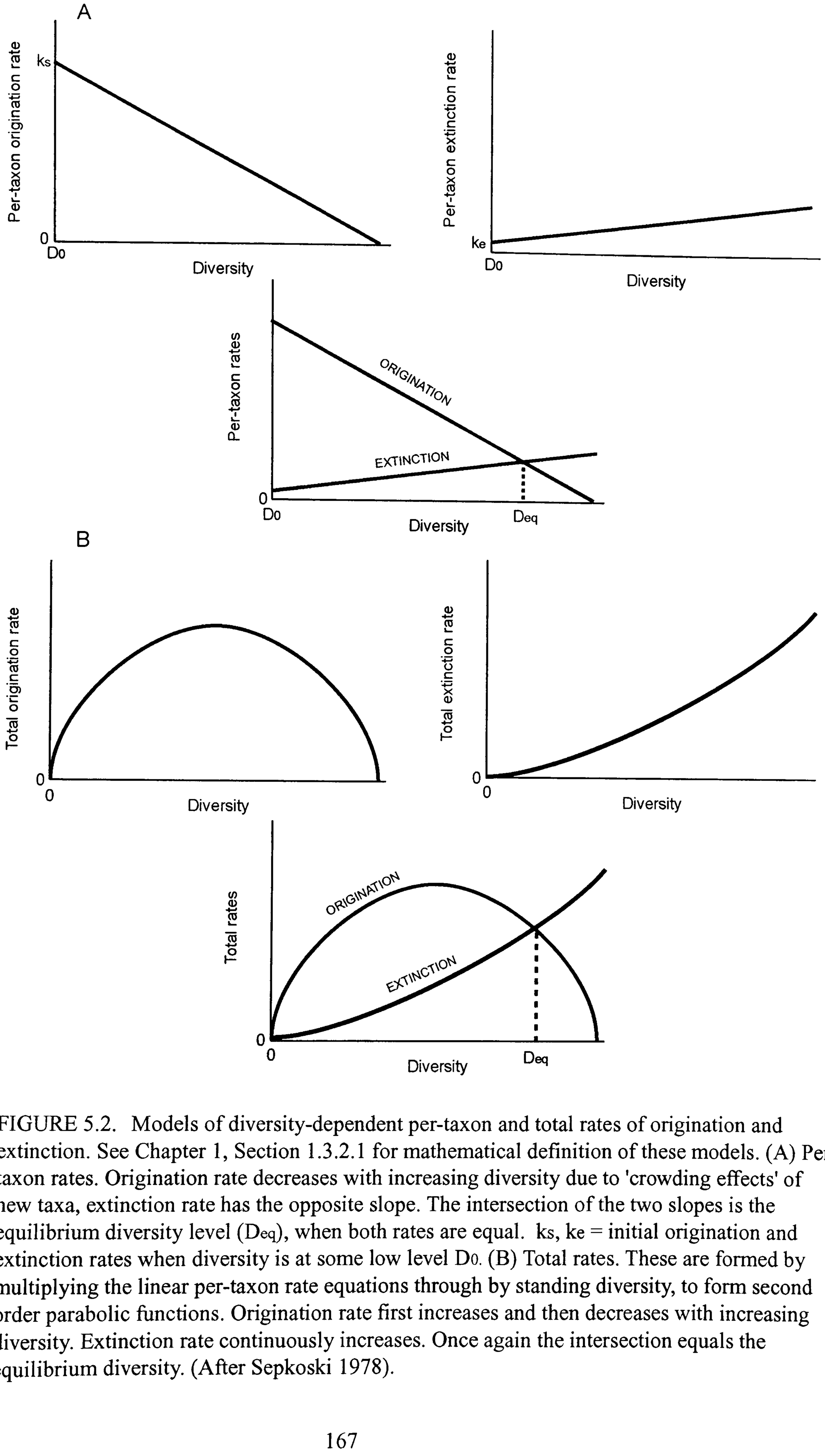


FIGURE 5.2. Models of diversity-dependent per-taxon and total rates of origination and extinction. See Chapter 1, Section 1.3.2.1 for mathematical definition of these models. (A) Per-taxon rates. Origination rate decreases with increasing diversity due to 'crowding effects' of new taxa, extinction rate has the opposite slope. The intersection of the two slopes is the equilibrium diversity level (D_{eq}), when both rates are equal. k_s, k_e = initial origination and extinction rates when diversity is at some low level D_0. (B) Total rates. These are formed by multiplying the linear per-taxon rate equations through by standing diversity, to form second order parabolic functions. Origination rate first increases and then decreases with increasing diversity. Extinction rate continuously increases. Once again the intersection equals the equilibrium diversity. (After Sepkoski 1978).

each other at equilibrium. They found no such correlation and hence concluded that the equilibrium model is false, preferring one of unfettered diversification interrupted by large scale environmental changes. Indeed Hoffman (1989) entirely rejected the idea of diversity-dependent origination and extinction rates at family level, and claimed that there is no evidence for the theory.

5.2. Analysis methods

5.2.1. Evolutionary rates

Three different origination and extinction rate measurements were plotted against standing diversity for marine taxonomic data from the Upper Cambrian to the end-Carboniferous. This time period corresponds to the diversity expansion and the majority of the 'equilibrium' period of the Palaeozoic plateau, and is the same as that analysed for diversity-dependence by Sepkoski (1979).

The rate measurements are:

- Total rates (R_s and R_e, number of events per million years)
- Per-taxon rates (r_s and r_e, number of events per lineage million years)
- Foote's (2000a) per-capita rates (p and q, number of events per lineage million years).

See Chapter 1, Section 1.2.1 for the mathematical definition of these rates. Calculations were performed using the TAXONOMIC database and associated SQL queries (See Chapter 3, Section 3.2.2 for description of the database). Results were obtained for marine taxa contained within the *Fossil Record 2* dataset (Benton 1993), and Sepkoski's (1992) marine family and unpublished genera datasets, for each of the stratigraphic intervals utilised by the relevant data sets. This gives a total of 25 data points for the *Fossil Record 2* data (Merioneth – Gzelian), and 26 for the Sepkoski data (Dresbachian – Stephanian). A previous study of the diversity-dependence of total origination and extinction rates for Post-Mid Cambrian Palaeozoic marine families (Sepkoski 1979) was based upon only 16 late Cambrian stages and Post-Cambrian Palaeozoic series. Standing diversity and rates data were calculated disregarding single-interval taxa (cf. Sepkoski 1996b, 1998b).

Foote's per-capita rates were used in addition to the more familiar per-taxon rates, as the latter are considered to be negatively correlated with interval length (Foote 2000a). Per-capita rates are based on 'boundary crossers', and are therefore unaffected by interval length (See Chapter 1, Section 1.2). However, if an interval has no taxa which range through it in entirety (Number of bottom and top crossers [Nbt] = 0), the per-capita rates cannot be resolved (Foote 2000b). This is because, for example in the case of origination rate, the proportion of taxa extant at the end of the interval that were also extant at the start (Nbt/Nt) is zero, as all top boundary crossers must have originated within the time interval. Foote's per-capita equations require the calculation of the natural logarithm of this ratio, which cannot be resolved for zero. Fortunately if the group is sufficiently large, as is the case here, this is only a problem at the extreme ends of a group's range (i.e. the first and last intervals).

To test for diversity-dependence within the data, Sepkoski's total and per-taxon rate diversity-dependent models, (as outlined in Chapter 1, Section 1.3.2.1, and Fig. 5.2), were given a least-squares fit to the appropriate data sets. The per-taxon rate models, which are simply first-order equations, were also given a least-squares fit to the per-capita origination and extinction rate results. For the diversity-dependent model to be accepted it must be shown that any correlations between standing diversity and origination/extinction rates are stronger than those displayed within stochastic data calculated from a stochastically generated model evolutionary tree. The CLOCKBACK program has been used to generate random phylogenies that display diversity patterns that mimic those of the Phanerozoic marine fossil record (See Chapter 4). For comparison with the empirical Palaeozoic marine origination and extinction rate data, a CLOCKBACK tree displaying an early diversity radiation followed by a 'plateau period' (Figure 4.5A) has had per-taxon rates of origination and extinction through time calculated. Per-capita rates are not required with the CLOCKBACK tree data as all time step intervals are of the same length, and are relatively short (intervals representing 5 million years) compared to the varying time-spans of the stratigraphic intervals in the empirical data. The correlations between the stochastic rate data and standing diversity were calculated for the period of diversity expansion and early equilibrium seen in the random tree. These correlations were then compared to those displayed by the empirical data.

Another useful datum to analyse is that of taxon longevity or lifetime (Newman and Sibani 1999). Taxon longevity for each marine taxon extant through the Palaeozoic

was established using the TAXONOMIC database, excluding uncertain interval assignments and singleton taxa. The mean longevity of all taxa extant in each Palaeozoic interval was then calculated and the results plotted through time, and also correlated with standing diversity. Mean taxon longevities cannot be calculated for intervals in the Meso-Cenozoic due to the upper limit of the Recent reducing extant taxon life spans as it is approached.

To focus the analysis of biodiversity dynamics onto the period of the Palaeozoic plateau itself, (i.e. the period of 'equilibrium' where standing diversity remains approximately constant through time), the following sets of marine generic data were plotted against time for the stages Caradoc (Upper Ordovician) to Leonardian (Lower Permian).

- Standing diversity
- Per-capita origination rate (p)
- Per-capita extinction rate (q)
- Per-capita diversification rate (p - q)
- Per-capita turnover rate (p + q).

Trend lines were fitted to display the long-term linear trend through time of each data set.

The correlation between origination and extinction rates through time can be used to investigate the diversity dynamics underlying empirical patterns. Here this relationship through the Palaeozoic plateau period has been assessed, firstly by correlating both origination and extinction per-capita rates with standing diversity for the stages Caradoc – Leonardian, and secondly by cross-correlating the rates. Because per-capita rates are normalised for both standing diversity and interval length, there should be no false correlation produced by the 'low-number effect' (Cowen and Stockton 1978) where intrinsically small numbers of origination and extinction events are produced during intervals of low diversity or short length. A proposed diagnostic characteristic of an equilibrium period is equal rates of origination and extinction through time, i.e. a diversification rate of zero; this should produce a positive correlation between the two rates (Flessa and Levinton 1975). However, the predictions of the logistic model do *not* require constant and equal origination and extinction rates, or a constant diversification rate of zero. In reality, diversity level will fluctuate around any

equilibrium, with rates fluctuating also. According to predictions of diversity dependence, when diversity climbs above the equilibrium level, origination rates will fall and extinction rates rise, resulting in a diversity fall. Similarly, if diversity drops below equilibrium, the opposite situation will occur, with origination rates rising and extinction rates falling (Sepkoski 1978). Therefore, the actual relationship should be a negative correlation, centered around the rate equality at equilibrium (Fig. 5.3B, C). If rates do not have a constant rate of change throughout the equilibrium period, the centre and the slope of the correlation between them will shift (Fig. 5.3D, E), and if this occurs to a significant degree many times throughout the equilibrium period any relationship will be difficult to discern, with data becoming chaotic. Without data of far higher stratigraphic resolution than is currently available for the global marine fossil record, such small-scale behaviour of the rates will be difficult to assess. However, taken over the whole equilibrium period, diversity climbs above the equilibrium should be just as likely as drops below, hence *mean* origination and extinction rates should equal one another, and *mean* diversification rate should be zero. To test this the mean values of all the above mentioned plateau period rate data sets were calculated. Kirchner and Weil (2000a) found a positive correlation between extinction rate and origination rates with a 10 million year time lag. To test the possibility that there may be a delay in the response of originations to extinctions, both contemporaneous rates, and extinction rates plotted against origination rates from two stratigraphic intervals later, have been correlated.

Once again the empirical data correlations have been compared with those seen in stochastic data using the CLOCKBACK randomly generated phylogeny. This time only those rates occurring through the actual 'plateau period' of the random tree were analysed and correlated, firstly with standing diversity, and secondly cross-correlated with each other.

Per-capita rates of marine origination and extinction were also calculated for the entirety of the Phanerozoic and plotted against time, to investigate their general trend, and any difference in the behaviour of these rates before and after the Permian extinction event. When plotting per-capita origination rate versus time through the Phanerozoic the two earliest Cambrian data points (N-Da and Tomm) have been excluded from both Sepkoski data plots. This is because the Tommotion, due to a low Nbt diversity (complete interval crossers) compared to high numbers of first appearances, has an extremely high origination rate, and therefore its inclusion distorts the Phanerozoic data curve.

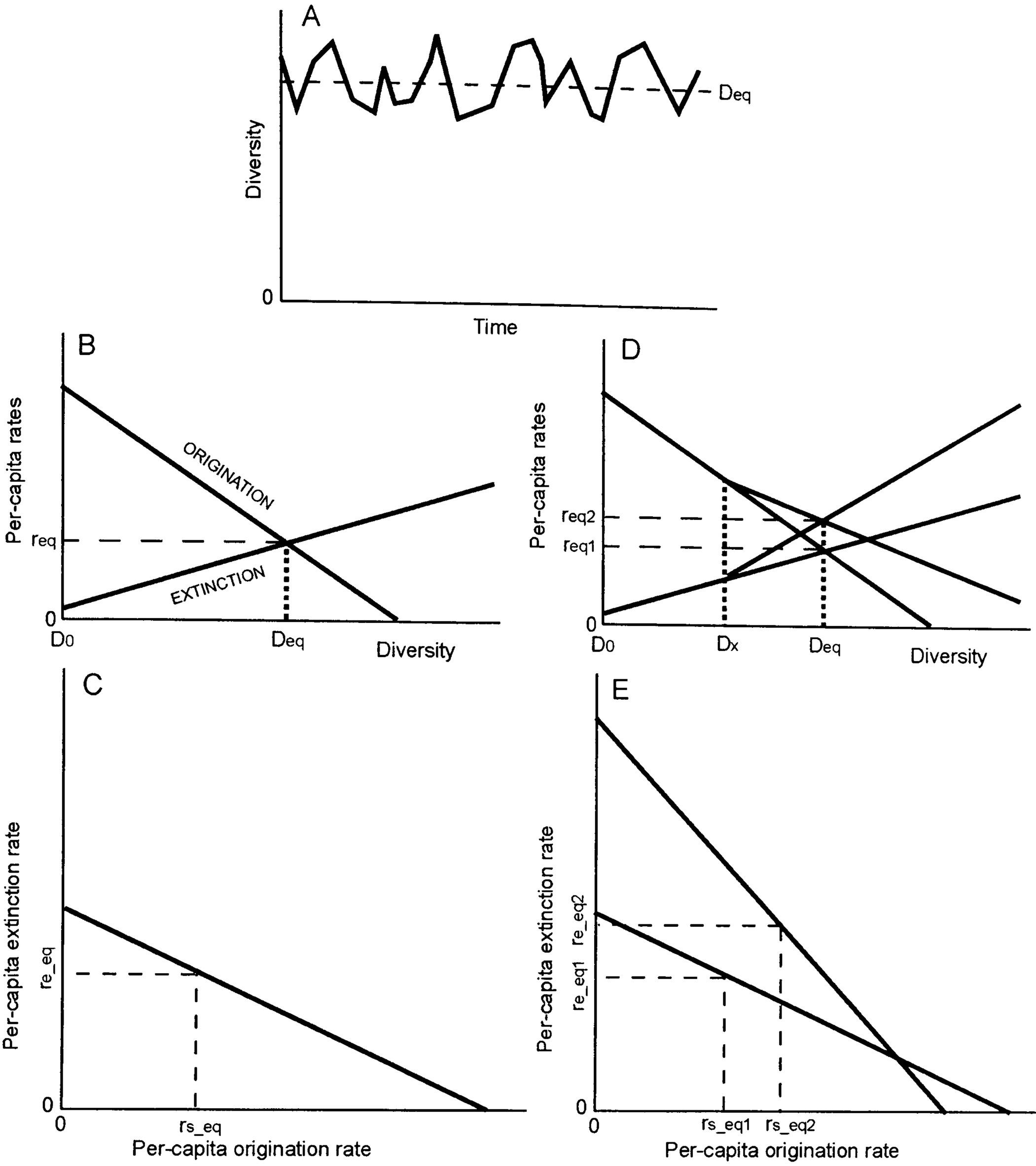


FIGURE 5.3. The diversity-dependent relationship between origination and extinction rate. (A) Hypothetical diversity curve with diversity levels fluctuating around an equilibrium value D_{eq} (B) Trends in origination and extinction rates with changing diversity. When diversity moves above the equilibrium level, origination rate will fall and extinction rate rise. The opposite occurs below the equilibrium. r_{eq} = the value of equal rates at equilibrium. (C) Hence origination and extinction rates are negatively correlated as diversity fluctuates around the equilibrium. Only when diversity equals the equilibrium value will the two rates equal each other ($r_{s\_eq} = r_{e\_eq}$). The slope of the relationship depends upon the relative slopes of the functions of changing rates with diversity, graph B. (D) If, at some diversity level D_x, the rates of change (slopes) of the functions are altered, a new value for rate equality at equilibrium will be set (r_{eq2}). (E) This will have the effect of shifting the correlation between origination and extinction rates and altering its slope. If this happens many times through the equilibrium period the resulting rates data will appear to be randomly distributed. However, if deviations of diversity above the equilibrium equal those below, the mean values of origination and extinction rate taken through the whole period will be equal.

5.2.2. Testing for competitive displacement

Clade diagrams or 'spindle diagrams' are an alternative to diversity/time graphs as a means of representing a group's diversity history (e.g. Sepkoski 1981; Bambach 1985). The shape of pairs of clade diagrams can be useful in indicating possible interactions between the two groups and the nature of any competitive displacement (Benton 1996). Figure 5.4 illustrates a range of theoretical shapes for co-existing pairs of clades, in which one clade ultimately survives and the other becomes extinct. A competitive displacement, however, may not require the complete extinction of one group. Sepkoski (1996a) presented theoretical 'double wedge' clade diagrams of the diversity histories of two competing but still extant clades, in his defence of the bivalves vs. brachiopods displacement (Fig. 5.5).

Spindle diagrams illustrating the familial diversity histories of the dominant marine classes have been constructed previously (Sepkoski 1981). Here a similar set of diagrams are constructed representing the generic diversity histories of the 21 dominant marine invertebrate classes through the Phanerozoic. These histories exclude single interval taxa. In addition, diagrams for these classes have been constructed for just the Palaeozoic period. The form of these diagrams can be compared with theoretical shapes to indicate possible pairs of candidates for large-scale competitive displacement or damping of diversity.

A purported case of competitive displacement in the marine realm is that of bivalves vs. articulate brachiopods (Sepkoski and Miller 1985; Sepkoski 1996a). Sepkoski (1996a) modeled the diversity histories of these two clades using coupled logistic equations which have inherent diversity damping and equilibria. However, it has also been suggested that these two groups do not display any long-term competitive interaction in their diversity histories, and the role of mass extinctions, in particular the end-Permian event, has been emphasised (Gould and Calloway 1980). Here an attempt is made to model the generic diversity histories of these two groups as exponential growth curves punctuated by mass extinction events equal in magnitude to those seen in the actual histories of the groups. The mass extinctions modeled are those regarded by Sepkoski (1996a, Fig. 9.14) as significant to the histories of bivalves and brachiopods. The diversification rate parameter of each group has been kept constant throughout model time, but the initial diversity parameter of the curve is re-set after every extinction event.

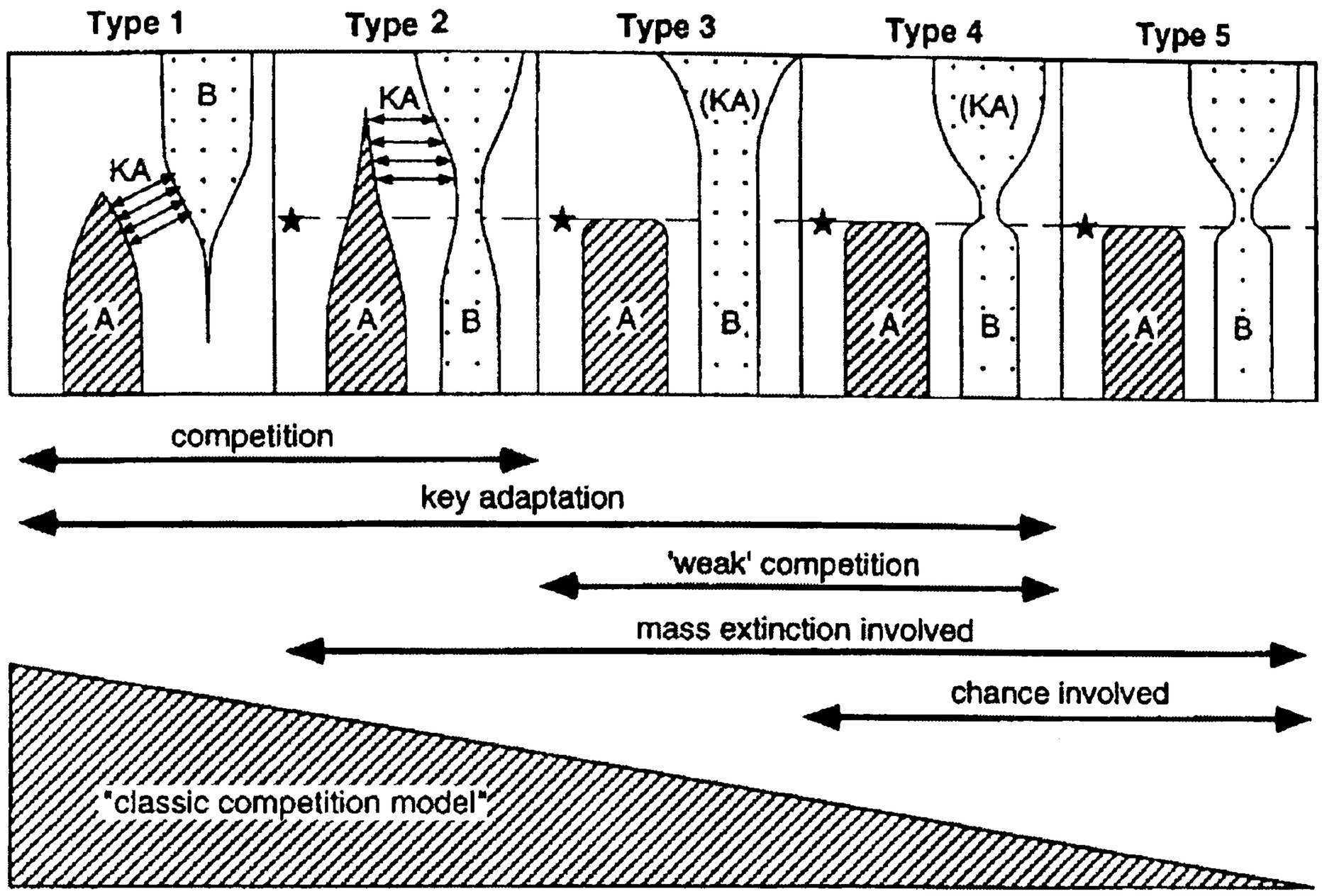


FIGURE 5.4. 'Double wedge' models of biotic replacement. The wedges represent the diversity waxing and waning of two co-existing clades, A and B. Moving left to right competitive interaction between the clades plays a decreasingly important role in the replacement, from the pure competitive displacement of type 1, to random chance in type 5. 'KA' indicates that a key adaptation is giving the incoming clade some advantage over the outgoing. Types 2 - 5 involve a mass extinction event which differentially affects the fortune of each clade. (After Benton 1996, Fig. 8.1.)

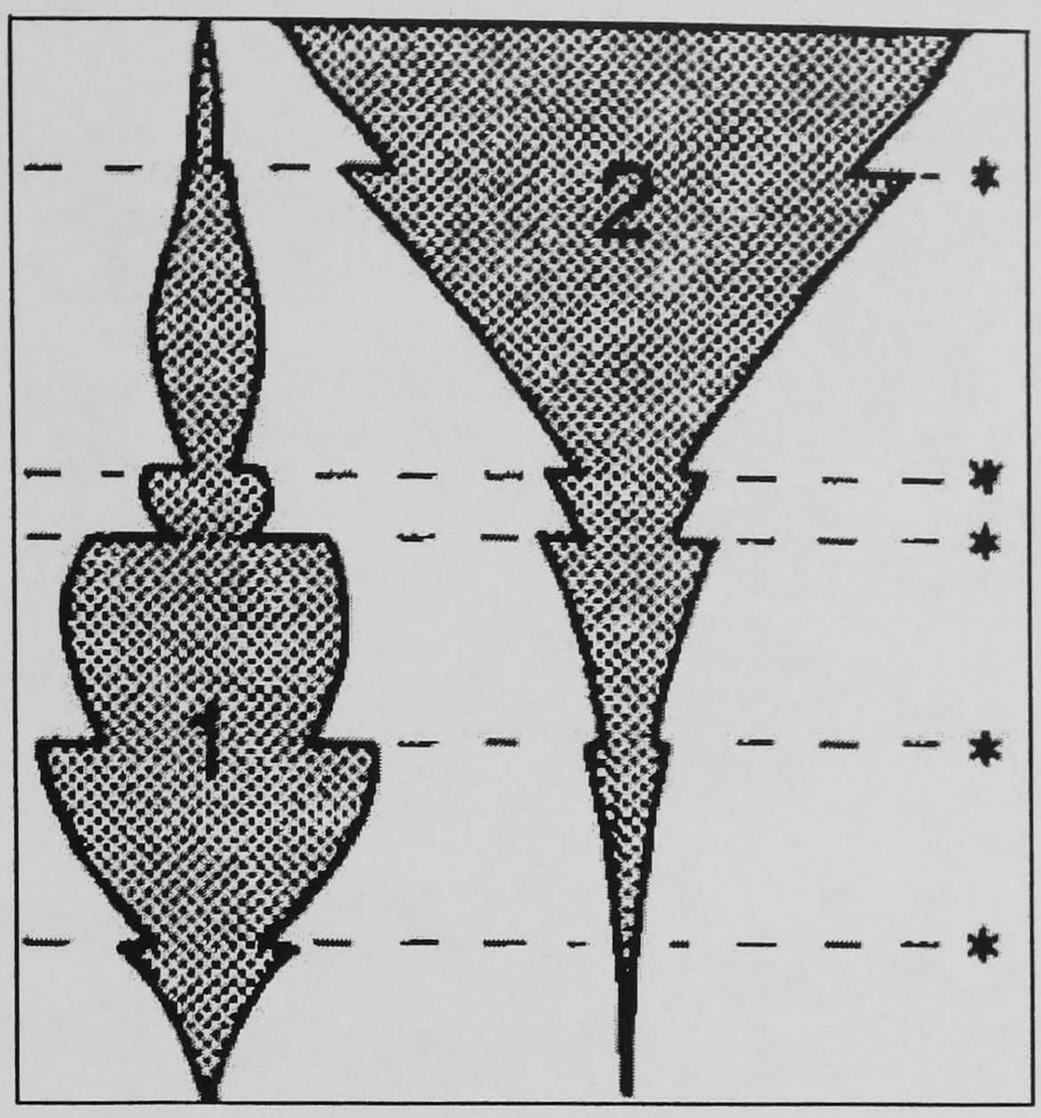


FIGURE 5.5. Double wedge model representing the logistic waxing and waning of two clades. Clades originate at the same time. Clade 1 has a higher per-taxon rate of origination, but a lower equilibrium diversity. Species of clade 2 thus replace clade 1. Both diversity patterns are perturbed by mass extinction events (indicated by asterisks). Sepkoski (1996) suggested that this model was comparable to the diversity dynamics of bivalves (clade 2) and articulate brachiopods (clade 1) (After Sepkoski 1996, Fig. 9.12).

Table 5.1. contains the modeled extinction events with their magnitudes as seen in articulate brachiopod and bivalve diversity histories. Neither the Ashgillian nor Serpukhovian events had much effect on bivalve diversity and so they are not modeled.

Extinction event	Approximate time period of event (mya)	Model duration (number of steps from start of model)	Magnitude (percentage diversity loss)	
			Articulates	Bivalves
Ashgillian	455 - 445	80 - 100	5%	-
Frasnian	395 - 360	180 - 200	76%	8%
Serpukhovian	335 - 315	220 - 240	32%	-
End-Permian	260 - 240	290 - 310	97%	68%
End-Triassic	225 - 205	330 - 350	49%	9%
Tithonian	165 - 150	390 - 410	43%	20%
End-Cretaceous	70 - 55	460 - 480	67%	48%

Table 5.1. Modeled mass extinction events for articulate and bivalve generic diversity. Timings and magnitudes of mass extinctions are calculated from Sepkoski's unpublished generic database.

The model is constructed over 530 time steps, representing 530 million years of evolutionary time. Very simply, a solution to the exponential diversification equation (Chapter 1, Equation 1.10) is created, with initial diversity set at 1 taxon, and an arbitrary diversification rate parameter. This is run until the first mass extinction event, when diversity is reduced by the magnitude set out in table 5.1. Exponential growth then recommences using the same diversification rate, but with the initial diversity reset to the standing diversity after the mass extinction. This process is repeated for all the mass extinction events and ends once 530 model time units have elapsed, representing 530 million years. Each extinction event takes up 20 time units, equivalent to 20 million years. Several model runs were completed with different diversification rates, until a system was achieved that most closely reproduced the diversity history of the group in terms of the diversity levels reached both before and after the end-Permian extinction event. This process was repeated to model both bivalve and articulate brachiopod diversification. The model assumes that mass extinctions are produced predominantly by forces extrinsic to the interaction between the two groups in question, and separate to the background extinction rate inherent in the diversification rate controlling the growth of the system. The shape of the resulting curve is greatly influenced by the mass extinctions, incorporating the idea that taxonomic diversification is generally expansive

but delayed by perturbations (Kitchell and Carr 1985). Therefore this model does not assume interaction between the two diversifying groups.

Finally the per-capita diversification rate and turnover rate histories of both articulate brachiopods and bivalves were calculated at generic level using the TAXONOMIC database, and analysed for any linear trends through time.

5.3. Results

5.3.1. Evolutionary rates

5.3.1.1. Testing diversity-dependent models

The results of the three measures of origination and extinction rate plotted against marine familial and generic diversity, for each stage from the Mid-Cambrian to the Upper Carboniferous, can be found in Figures 5.6 – 5.8. The form of the fit of Sepkoski's diversity-dependent models to the data for each rate is shown, in addition to the correlation coefficients for each fit. The results of the correlations between stochastic diversity and rates for the CLOCKBACK randomly generated phylogeny are shown in Figure 5.9. All correlation coefficients are summarised in Table 5.2.

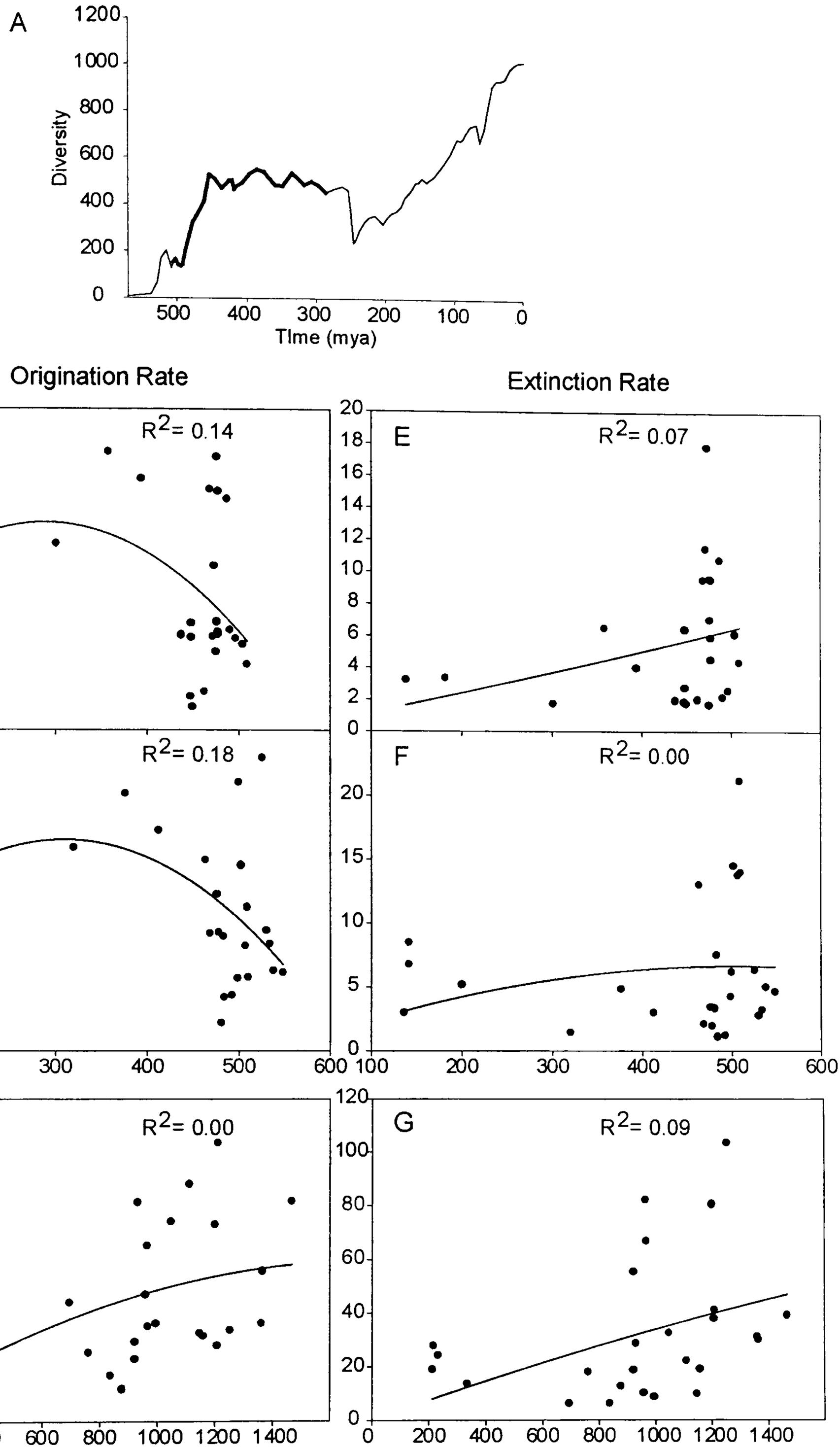


FIGURE 5.6. The relationship between total rates of marine origination/extinction and diversity. Upper Cambrian to End Carboniferous. (A) Marine familial diversity curve with time period under analysis shown in bold. (B, E) Marine families. Data from Benton (1993) (C, F) Marine families. Data from Sepkoski (1992). (D, G) Marine genera. Data from Sepkoski (unpub.). Total origination and extinction rates are in units of taxa per million years. Each data set has the diversity-dependent total origination/extinction rate equation fit. Correlation coefficients are shown.

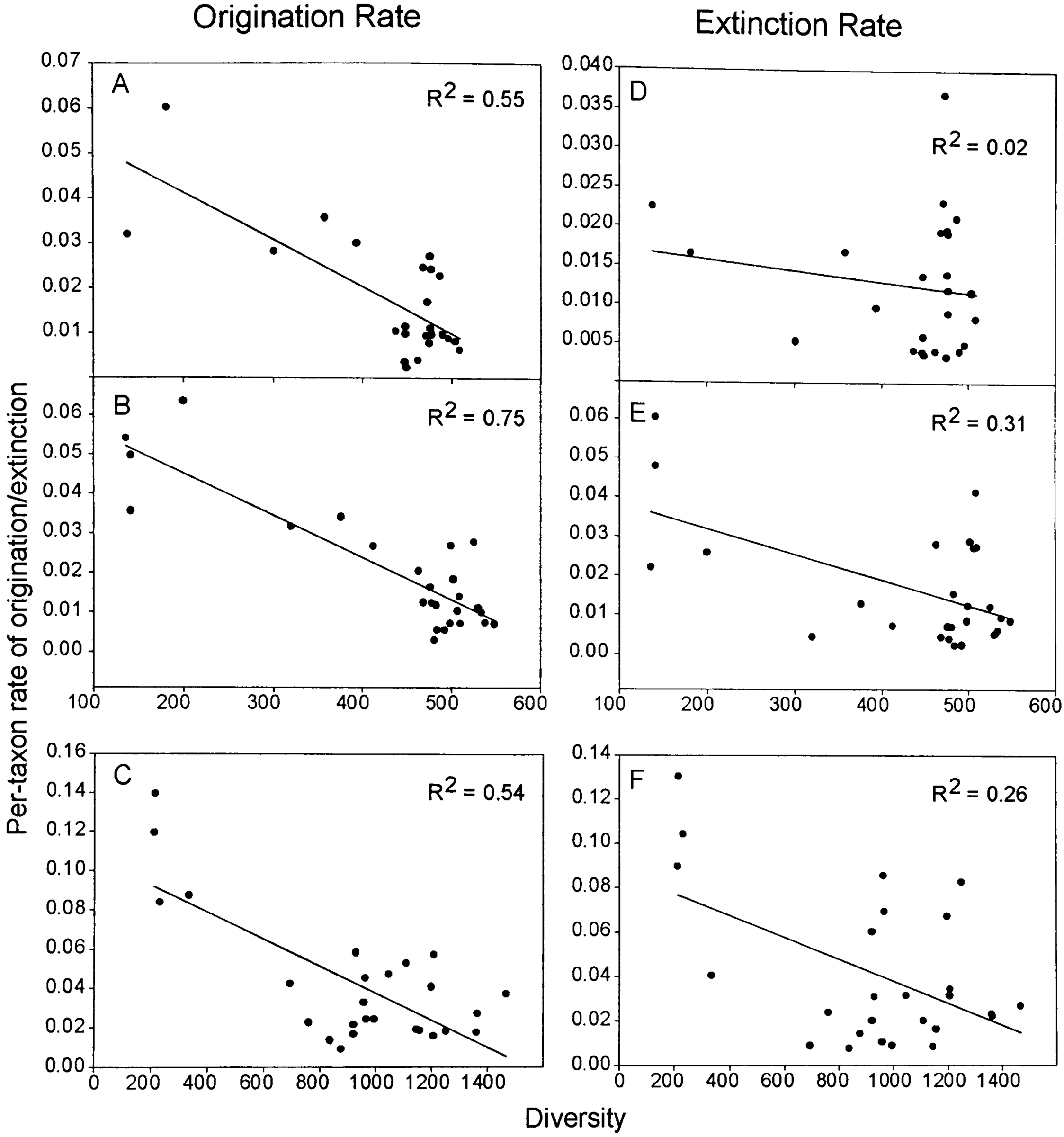


FIGURE 5.7. The relationship between per-taxon rates of origination/extinction and diversity. Upper Cambrian to End-Carboniferous. (A, D) Marine families. Data from Benton (1993) (B, E) Marine families. Data from Sepkoski (1992). (C, F) Marine genera. Data from Sepkoski (unpub.). Per taxon origination and extinction rates are in units of taxa per Lmy. Each data set has the diversity-dependent per-taxon origination/extinction rate equation fit. Correlation coefficients are shown.

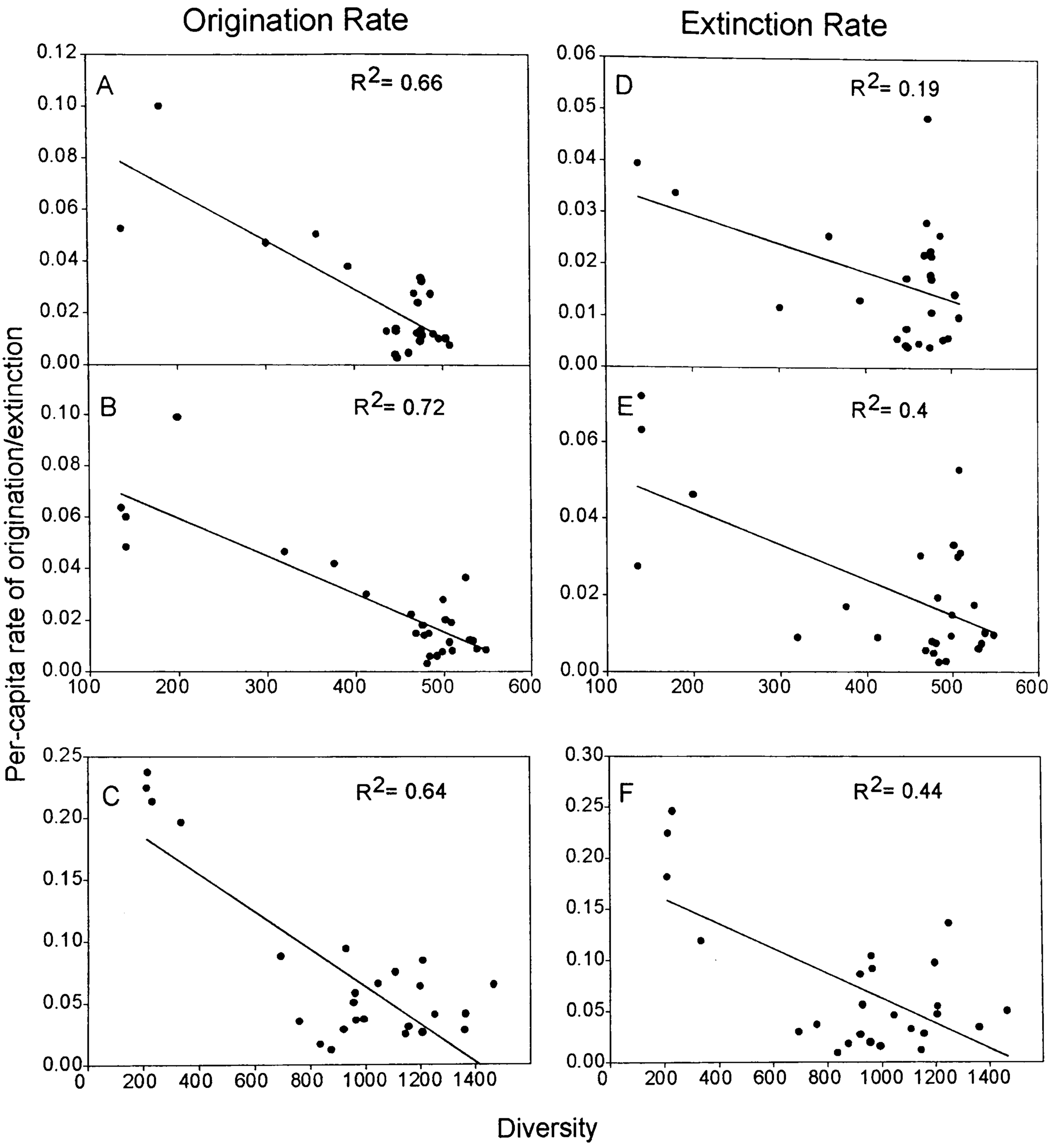


FIGURE 5.8. The relationship between per-capita rates of origination/extinction and diversity. Upper Cambrian to End-Carboniferous. (A, D) Marine families. Data from Benton (1993) (B, E) Marine families. Data from Sepkoski (1992). (C, F) Marine genera. Data from Sepkoski (unpub.). Total origination and extinction rates are in units of taxa per Lmy. Each data set has the diversity-dependent per-taxon origination/extinction rate equation fit. Correlation coefficients are shown.

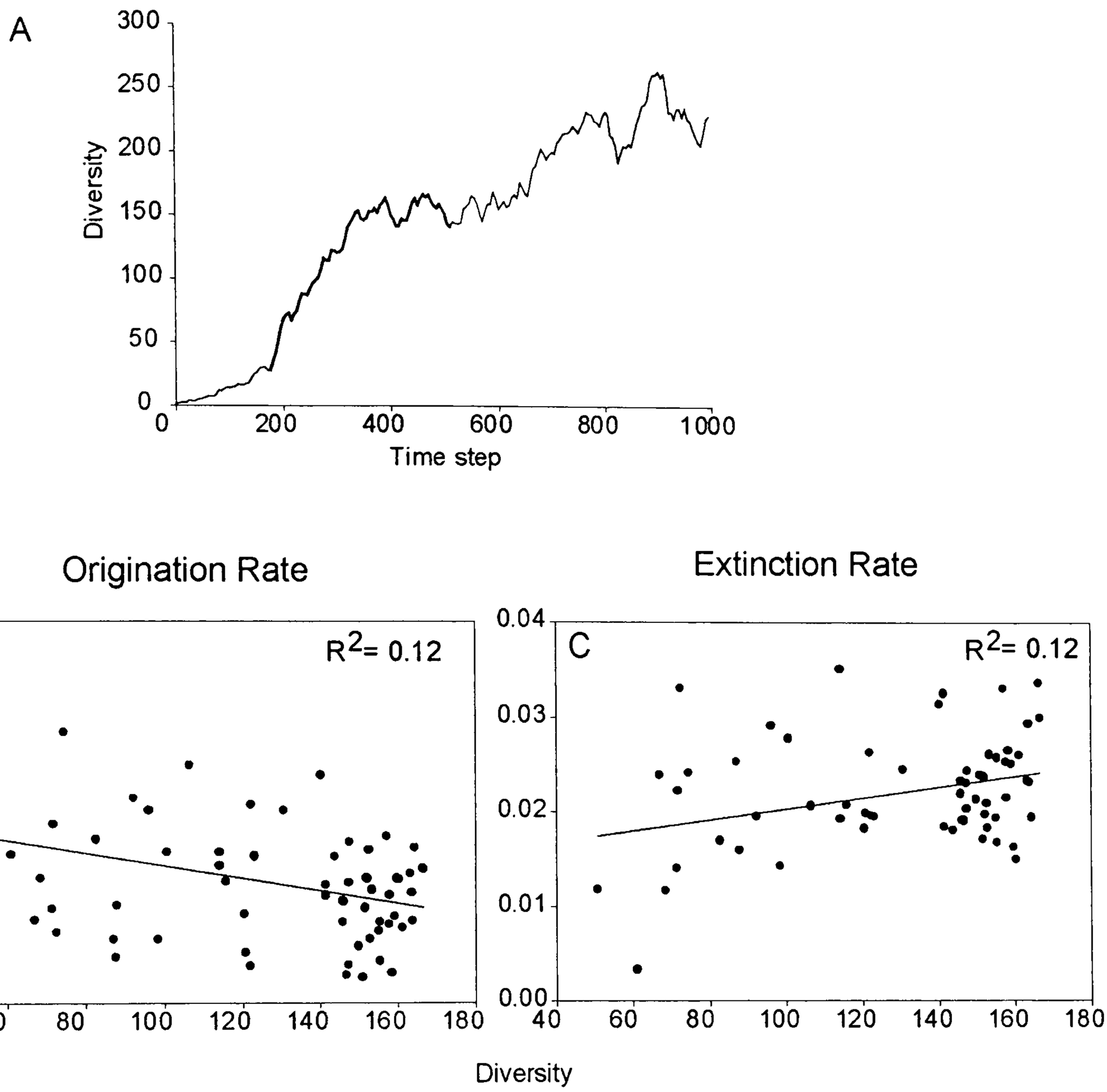


FIGURE 5.9. Stochastic diversity and rate data: diversity expansion to equilibrium. (A) Diversity curve of a randomly generated tree from the CLOCKBACK program, modelling the Phanerozoic marine diversity pattern. The time period under analysis is shown in bold. (B) Per-taxon origination rate data from the CLOCKBACK tree correlated with diversity for each time step of the period shown. (C) Per-taxon extinction rate data from the CLOCKBACK tree correlated with diversity for each time step. Rates are in units of taxa per taxon standing diversity per time step. Correlation coefficients are shown.

Model fit	Rate correlated with standing diversity	Data set	Correlation coefficient (R^2)
Diversity-dependent - 2nd order least-squares fit	Total origination rate	Benton 1993	0.14
		Sepkoski 1992	0.18
		Sepkoski unpub.	0.00
	Total extinction rate	Benton 1993	0.07
		Sepkoski 1992	0.00
		Sepkoski unpub.	0.09
Diversity-dependent - 1st order least-squares fit	Per-taxon origination rate	Benton 1993	0.55
		Sepkoski 1992	0.75
		Sepkoski unpub.	0.54
	Per-taxon extinction rate	Benton 1993	0.02
		Sepkoski 1992	0.31
		Sepkoski unpub.	0.26
	Per-capita origination rate	Benton 1993	0.66
		Sepkoski 1992	0.72
		Sepkoski unpub.	0.64
	Per-capita extinction rate	Benton 1993	0.18
		Sepkoski 1992	0.04
		Sepkoski unpub.	0.44
	Per-taxon origination rate	CLOCKBACK tree	0.12
	Per-taxon extinction rate	CLOCKBACK tree	0.12

Table 5.2. Models, data and correlation coefficients testing diversity dependence. The fit of the models to empirical and stochastic origination and extinction rate/diversity data for the Cambrian to the Upper Carboniferous is shown.

Total origination/Extinction rates

The fit of the diversity-dependent total origination rate model to both familial data sets is poor (Fig. 5.6B, C). There is a wide spread of data around the form of the model, the data points at higher diversities, i.e. the data for stages after the Cambro-Ordovician radiation, range from a high of nearly 15 new families per million years in the Caradoc down to a low of just over 1 new family per million years in the Stephanian (Sepkoski 1992 data). The rate values in between these two extremes appear to contain little more organisation than random data. The form of the model fit, however, does display a slight parabolic curve as expected by the Sepkoski model (Fig. 5.2B). At generic level (Fig. 5.6D) there is no fit of the model at all; the data display a wide spread with little discernible trend.

The model fits for total extinction rates are even less convincing (Fig. 5.6E – G), with the upwardly concave form of the model (Fig. 5.2B) not apparent. The R^2 values for each fit are low, although that for generic total extinction rate is higher than generic origination rate.

Hence, the total rates diversity-dependent models do not appear to be a good description of the data at family and genus level. However, total origination and extinction rate measurements are not normalised for diversity. Sepkoski's models reflect this in expecting a non-linear trend in these rates with increasing diversity. Despite this the high total rates inevitably produced at high diversity levels may reduce the fit of the model. Therefore, rates normalised for diversity level (per-taxon and per-capita rates) may provide a better test of diversity-dependence.

Per-taxon origination/extinction rates

The fits of the diversity-dependent model to per-taxon origination rate data (Fig. 5.7A-C) are considerably better than those of the total rates data. The fit for per-taxon extinction rates is also an improvement (Fig. 5.7E-F), but the form of the model, which is simply a linear change with diversity level, displays the opposite slope to that predicted (Fig. 5.2A). The Diversity-dependence theory of Sepkoski expects per-taxon extinction rate to display a positive trend with increasing diversity, as species crowding and competition lead to greater numbers of extinctions (Sepkoski 1978, 1979). Conversely, the empirical data show that per-taxon extinction rates have a weak negative linear trend with increasing diversity, similar to, although not as strong as, that seen in origination rates.

Per-capita origination/extinction rates

The data for per-capita rates (Fig. 5.8) display similar results to those seen in the per-taxon rates, although the fit of the linear model to extinction rates is slightly stronger. Again, however, the extinction rates display the opposite trend to that expected – rates decrease with increasing diversity. Origination rates provide an adequate fit, with 64-72% of the variation in data being described by the diversity-dependent model. Origination rates display the expected trend of a decrease in the rate of appearance of new taxa with increasing diversity level. This trend is evident in both family and genus data.

Origination rates, both per-capita and per-taxon, display considerably stronger correlation coefficients for the fit of the diversity-dependent model than those seen in the stochastically generated data of the CLOCKBACK tree (Table 5.2 and Figure 5.9). Extinction rate data show slightly stronger correlations than those of the random data, but the slopes of the extinction rates fits are the opposite to those predicted. Therefore, it can be concluded that origination rates display the expected diversity-dependent behaviour during the Cambro-Ordovician radiation through to the early equilibrium of the Palaeozoic. There is no evidence for positive diversity-dependence in extinction rates, although there is a weak negative correlation suggesting extinction rates decrease with increasing diversity.

5.3.1.2. Taxon longevity through the Palaeozoic

The graphs in Figure 5.10 display mean taxon longevity for each stratigraphic interval through the Palaeozoic. Each data point represents the mean lifetime of all the marine taxa that have a presence in the interval, excluding singletons. Therefore the total lifespan of a taxon will be included in the interval calculation regardless of whether it has just originated, will imminently go extinct, or is in the middle of its time range.

Low mean family longevities (below 50 myrs) are not apparent in the *Fossil Record 2* data (Fig. 5.10A). Very low longevities are generally found among Cambrian taxa. As the *Fossil Record 2* only has three Cambrian intervals, very short-lived families are confined to one interval and therefore discarded as singletons. The exclusion of these taxa increases the overall mean longevities for the Cambrian intervals. Despite this anomaly, the pattern of mean taxonomic longevity through the Palaeozoic is very similar across data sets and for both family and generic data. There is a steady increase through the Period from low longevities in the Cambrian to high in the Permian. The trend appears linear, although there is a suggestion in the Sepkoski family data that the trend levels out in the later Palaeozoic (Fig. 5.10B). There are also greater fluctuations in the generic data (Fig 5.10C). An interesting point to note is the sudden jump in mean taxon longevity evident in the Latest Permian stage in all three data sets. This seems counter-intuitive as one would expect taxonomic longevity to decrease during a mass extinction event. However, it can be explained as the result of low standing diversity produced by the extinction event, combined with the apparently above average life spans of those few taxa that do survive across the Permo-Triassic boundary. The

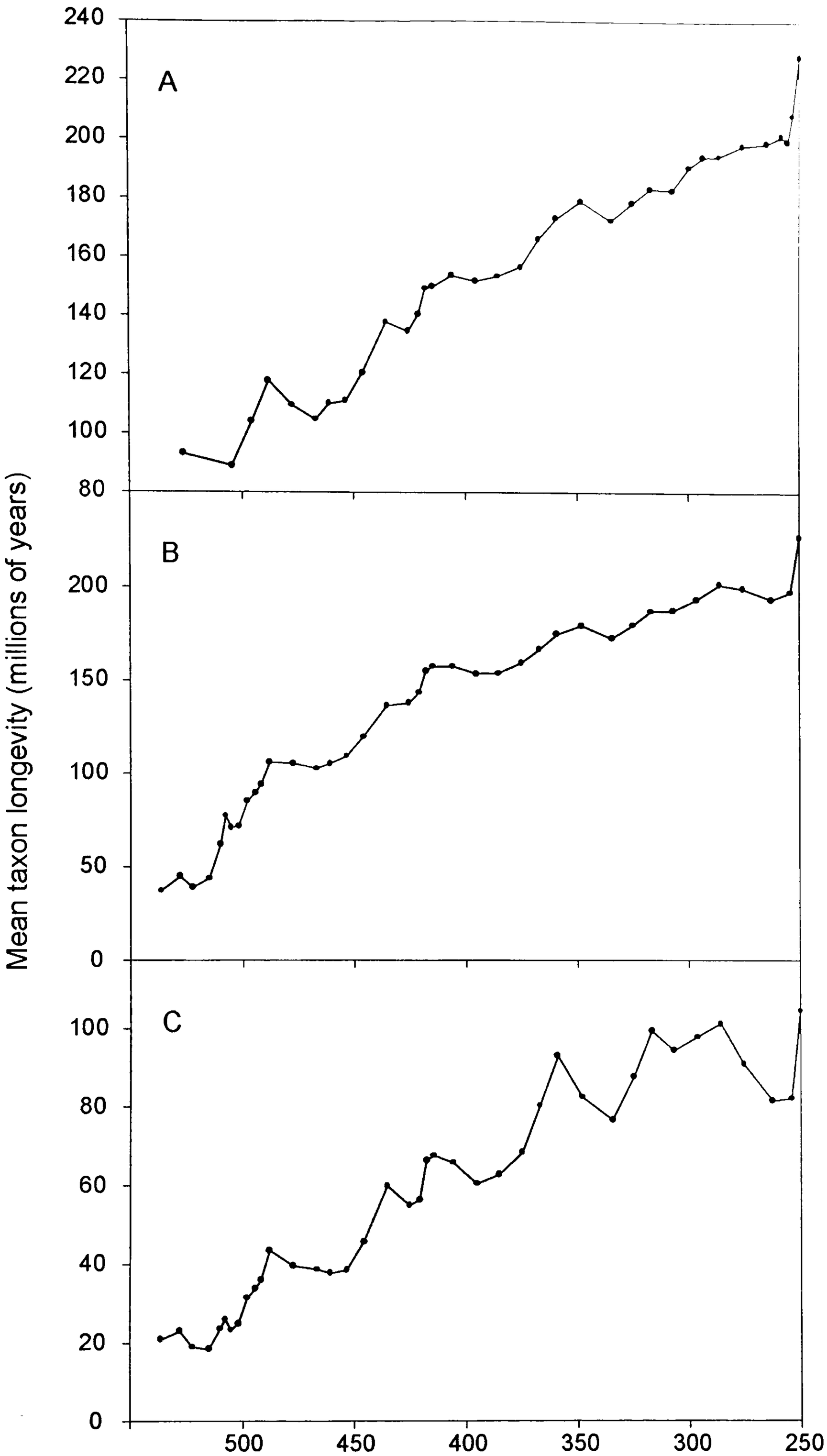


FIGURE 5.10. Mean taxon longevity through the Palaeozoic. (A) Marine families. Data from Benton (1993) (B) Marine families. Data from Sepkoski (1992). (C) Marine genera. Data from Sepkoski (unpub.). Each stratigraphic interval through the Palaeozoic has a data point indicating the mean lifespan of all the taxa (excluding singletons) with a presence in that interval.

shortening effect of the Permian extinction event on taxonomic longevity seems to be most evident in those stages leading up to the event, certainly in the Sepkoski data sets (Fig. 5.10C, D), although this is not so obvious in the *Fossil Record 2* data (Fig. 5.10A). Figure 5.11 illustrates the correlation between marine standing diversity and mean taxonomic longevity for Palaeozoic intervals. As should perhaps be expected with the correlation between a linear trend through time (taxon longevity) with a non-linear (standing diversity) the correlation is fairly weak, except in the Sepkoski family data set (Fig. 5.11B). Here the correlation is reasonable ($R^2 = 0.65$) and is due to the more logistic form of the mean taxon longevity curve (Fig. 5.10B) mentioned above.

Therefore, from the low marine diversities of the Cambrian, through the Ordovician rise and the subsequent higher diversity levels of the rest of the Palaeozoic, taxonomic life spans were gradually increasing in length as extinction rates decrease.

5.3.1.3. Evolutionary rates through the Palaeozoic plateau period

Trends in diversity and rates through the plateau period

Trends in marine generic diversity levels and per-capita evolutionary rates through exclusively the period of diversity 'equilibrium' in the Palaeozoic (Caradoc – Leonardian) are shown in Figure 5.12. The mean values of each evolutionary rate (origination, extinction, diversification and turnover) are shown and also contained in Table 5.3.

Origination rate	Extinction rate	Diversification rate	Turnover rate
0.037	0.045	– 0.007	0.082

Table 5.3. Marine generic rates through the Palaeozoic plateau period (Caradoc-Leonardian). Singleton genera excluded. Mean per-capita rates are in units of genera per Lmy.

The fact that generic marine diversity does *not* display a level equilibrium, as identified in Chapter 3, Section 3.3.1, is highlighted by the curve and fitted trend line in Figure 5.12A. The actual trend is one of a gentle decline in diversity, from nearly 1500 genera in the Mid-Ordovician to just over 1000 in the Mid-Permian. Large fluctuations are evident around this trend. Both per-capita origination rate and per-capita extinction

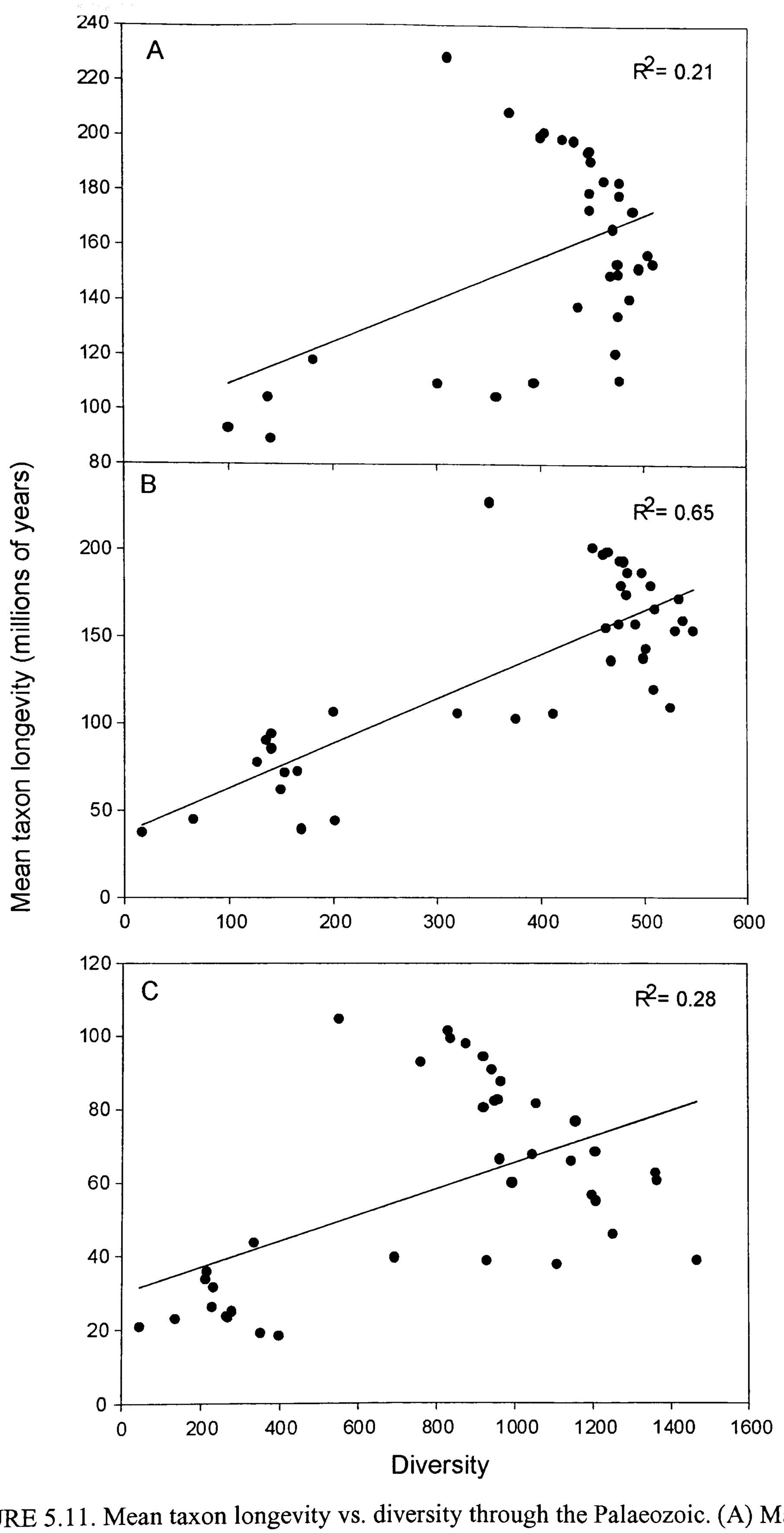


FIGURE 5.11. Mean taxon longevity vs. diversity through the Palaeozoic. (A) Marine families. Data from Benton (1993). (B) Marine families. Data from Sepkoski (1992). (C) Marine genera. Data from Sepkoski (unpub.). A linear least-squares correlation has been fit through each data set, the correlation coefficients are given.

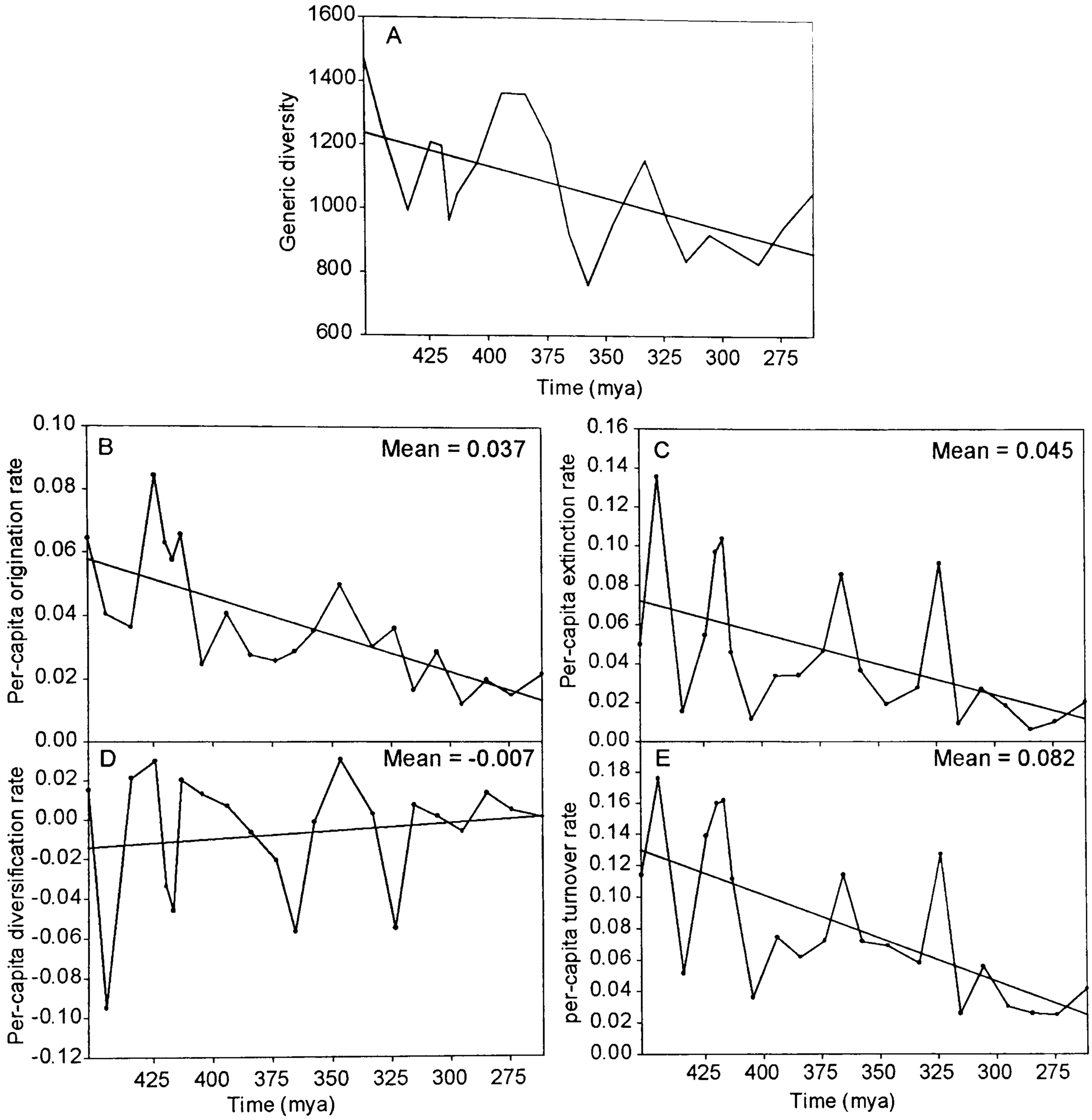


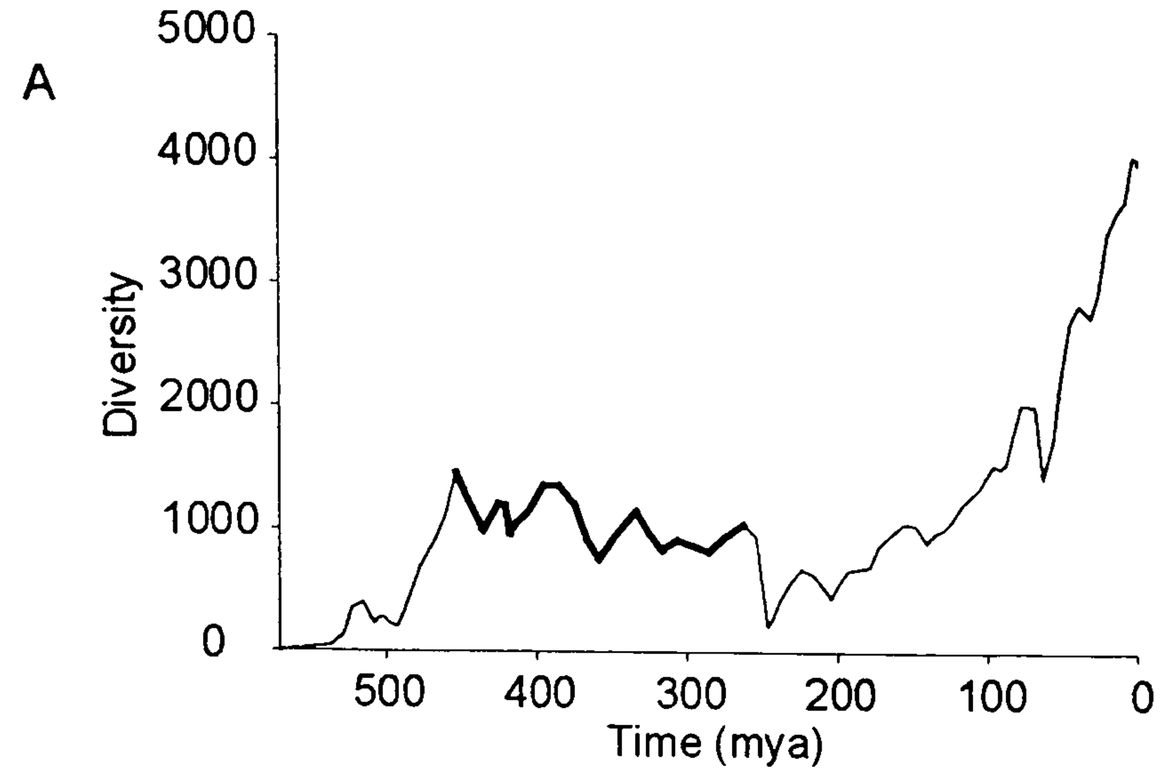
FIGURE 5.12. Generic diversity and per-capita rates through the Palaeozoic 'equilibrium' period (Caradoc - Leonardian). Data from Sepkoski (unpub.), excludes singletons. (A) Standing diversity. (B) Origination rate. (C) Extinction rate. (D) Diversification rate. (E) Turnover rate. Linear trend lines are fitted to curves A-E. Mean rates are given. All rates are in units of genera per Lmy.

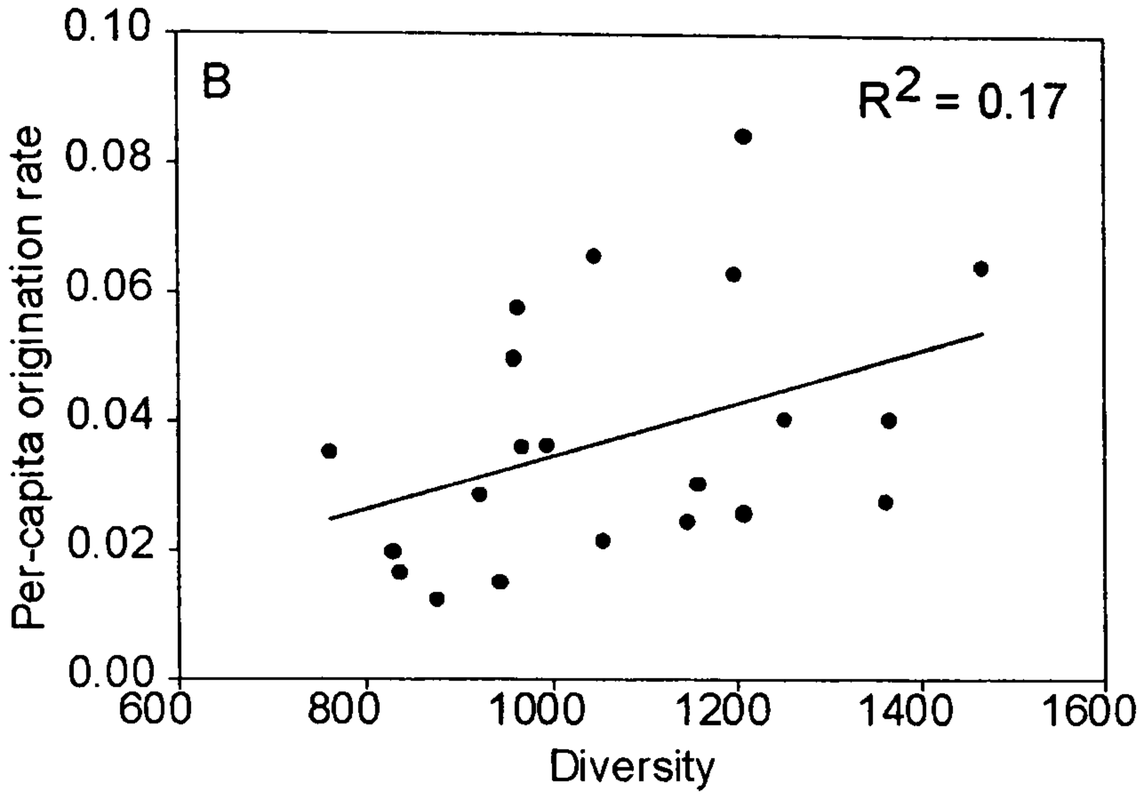
rate show a decrease in value through the period of the 'plateau', with the slope of the extinction rate decline being the steeper (Fig. 5.12B, C). The two rates near equality at the end of the curves. The mean extinction rate (0.045 genera per Lmy) is higher than mean origination rate (0.037 genera per Lmy). This difference, with the marine biota experiencing on average more extinctions than originations, result in a diversification rate that averages below zero (-0.007), and explains the overall decline in generic diversity. Despite this, the diversification rate shows a slight positive trend. As a result, the generic decline in diversity is linear, rather than exponential, which would be the case if the diversification rate remained at a constant negative value. The trend of diversification rate towards zero, as origination and extinction rates near equality, could be interpreted as a trend towards diversity-dependent behaviour and true equilibrium, a situation that would have been achieved in time in the absence of the End-Permian extinction. If so, then the equilibrium would be achieved after a period of *declining* diversity, which is contrary to the predictions of the logistic model.

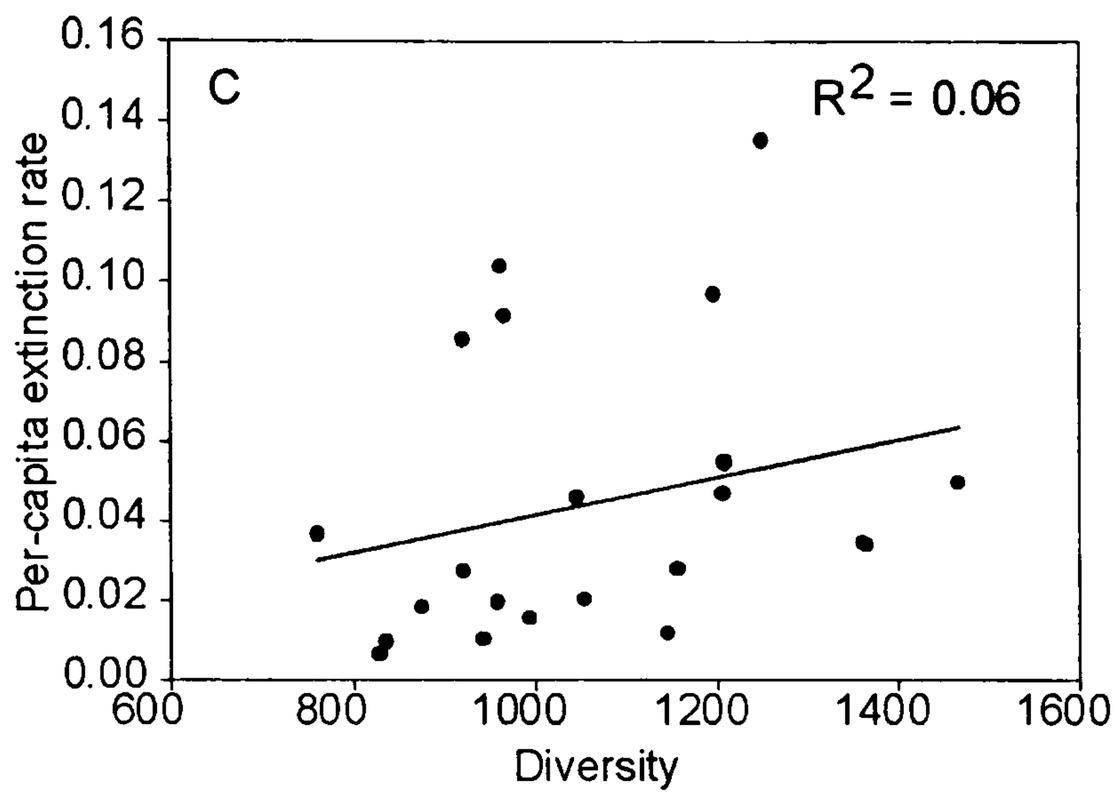
The declining turnover rate through the plateau period is a combination of the negative trends in origination and extinction rates. It is also reflected by the increase in species longevity identified above. Hence, the combined results of these graphs provides evidence that the generic diversity system of the later Palaeozoic became less dynamic through the period, with lower turnover and longer taxonomic life spans.

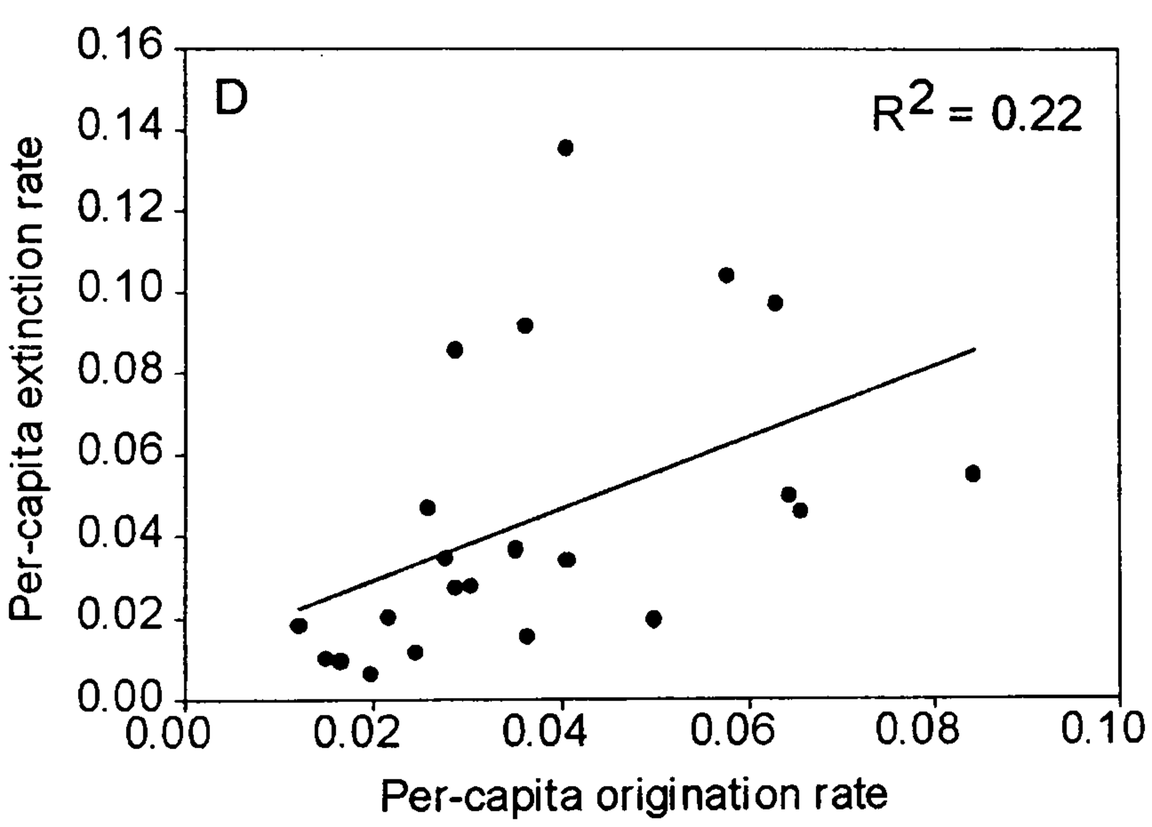
Correlations between diversity and rates through the plateau period

The results given in Section 5.3.1.1. demonstrate a reasonably strong negative correlation between origination rates and standing diversity over the period of diversity expansion and equilibrium through the Palaeozoic (Upper-Cambrian – End-Carboniferous), but only a weak negative correlation between extinction rates and diversity (Figs. 5.7, 5.8). This leads to the conclusion that origination rates are diversity-dependent over this period. However, the same correlations for solely the Palaeozoic plateau period (Caradoc-Leonardian), illustrated in Figure 5.13B and C, indicate that during these stratigraphic intervals neither rate is well correlated with diversity (R^2 values of 0.17 and 0.06 for origination and extinction rates respectively). These correlations are only marginally stronger than those found between diversity and rates within the 'plateau period' of the stochastically generated CLOCKBACK tree (R^2 of 0.05 for origination rate and 0.02 for extinction rate), see Figures 5.14B and C. Therefore, origination rate appears to be diversity dependent over the Late Cambrian









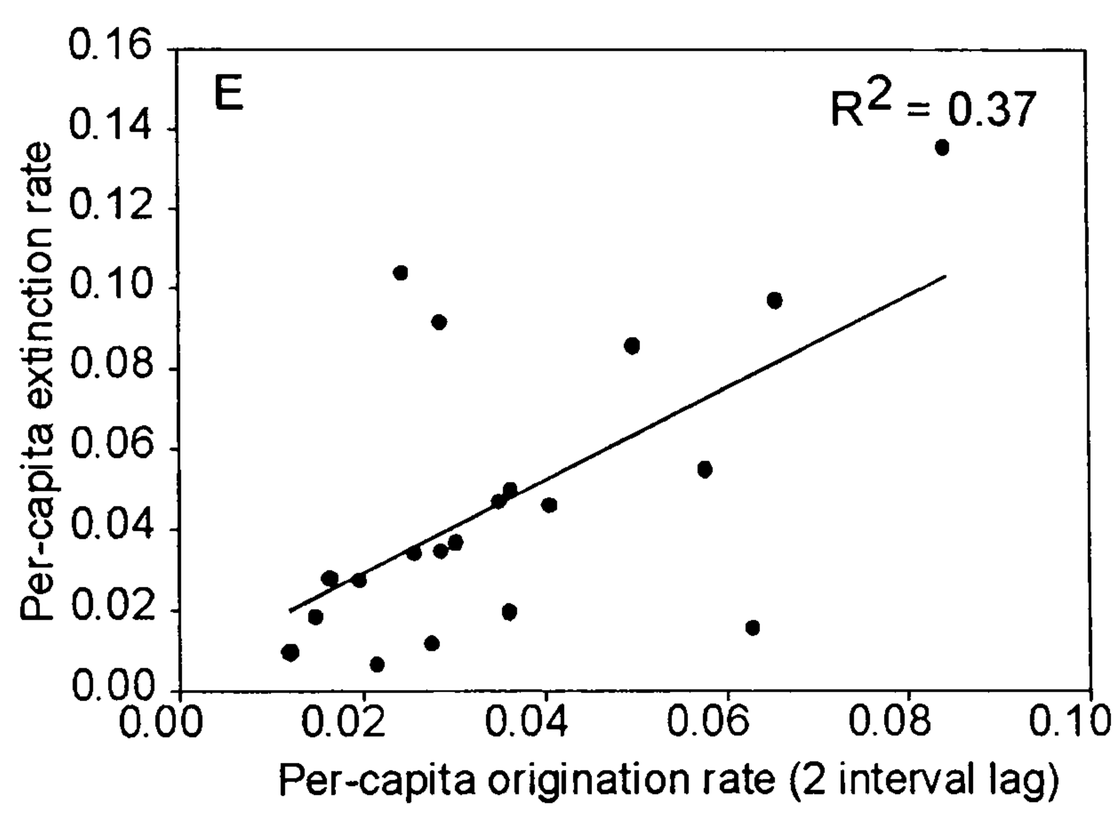


FIGURE 5.13. Generic diversity vs. rate correlations through the Palaeozoic 'equilibrium' period (Caradoc - Leonardian). Data from Sepkoski (unpub.), excludes singletons. (A) Marine generic diversity curve with time period of analysis shown in bold. (B) Origination rate versus diversity. (C) Extinction rate versus diversity. (D) Extinction rate versus contemporaneous origination rate. (E) Extinction rate versus origination rate with a two interval lag. Correlation coefficients are given. All rates are in units of genera per Lmy.

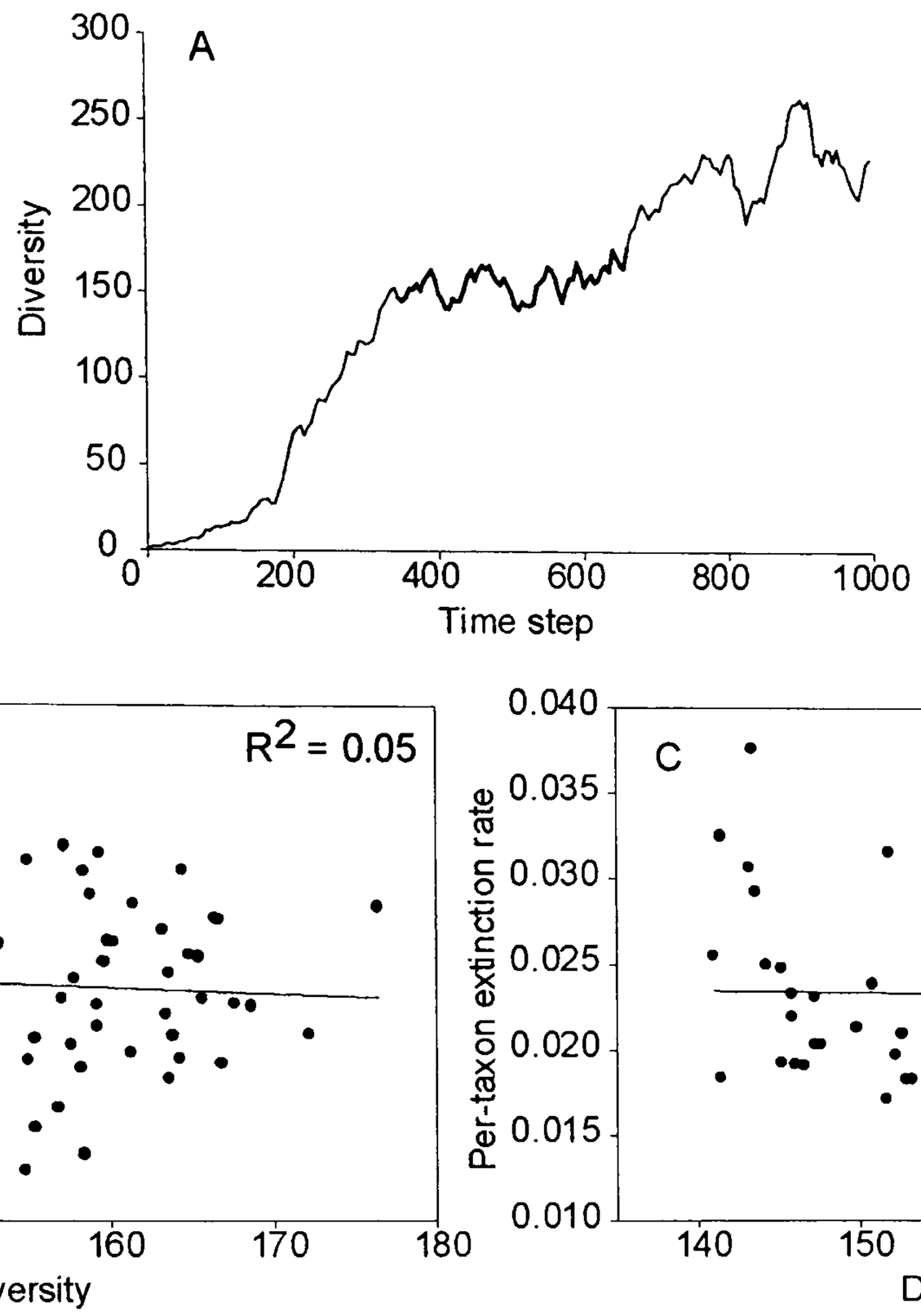


FIGURE 5.14. Stochastic diversity and rate data: diversity equilibrium period. (A) Diversity curve of a randomly generated tree from the CLOCKBACK program, modelling the Phanerozoic marine diversity pattern. The time period under analysis is shown in bold. (B) Per-taxon origination rate data from the CLOCKBACK tree correlated with diversity for each time step of the period shown. (C) Per-taxon extinction rate data from the CLOCKBACK tree correlated with diversity for each time step. (D) Per-taxon origination rate correlated with contemporaneous extinction rate. Rates are in units of taxa per taxon standing diversity per time step. Correlation coefficients are shown.

and Ordovician diversity rise to the high of the plateau, but diversity independent over the plateau period itself, indicating either the lack of a dynamic equilibrium, or a very broadly defined equilibrium diversity level. It could be that the rather weak correlation of origination rate with diversity over the plateau period may be due to diversity during the Palaeozoic consisting of an amalgamation of different evolutionary faunas, each with its own characteristic rate. This requires further testing. As argued in section 5.2.1 above, there should be an overall negative correlation between origination and extinction rates through an extended dynamic equilibrium period, as the two rates are the inverse of each other during fluctuations above and below the equilibrium level. Figure 5.13D demonstrates that this is not the case for generic per-capita origination and extinction rates through the Palaeozoic plateau period, but that they show a weak positive trend (R^2= 0.22) as both decline contemporaneously. A slightly stronger positive correlation (R^2= 0.37) is apparent when a lag time of two stratigraphic intervals is introduced from the extinction to the origination rate (Fig. 5.13E). Hence there is evidence that extinction events are driving origination events, which supports Kirchner and Weil's (2000a) suggestion of a lag time in the reaction of new originations to extinctions events. However, both correlation of contemporaneous rates and of lagged rates are weak, only slightly stronger than that between the CLOCKBACK tree rates (R^2 = 0.08, Fig. 5.14D), demonstrating that Palaeozoic plateau origination and extinction rates display little more of a relationship than would be expected in random data. This could be attributed to a shift in the equilibrium rates equality value through the Palaeozoic, which would lead to patterns of data that appear random (see Fig. 5.3D, E). However, as shown in Table 5.2, mean generic per-capita rates through the Palaeozoic display a marked difference and therefore diversification rate does not average to zero. Hence, the expectations of a state of dynamic equilibrium at generic level from the Caradoc to the Leonardian are not supported by this evidence.

Origination and extinction rates throughout the Phanerozoic

The curves displayed in Figure 5.15 show the trends in per-capita origination and extinction rates throughout the entire Phanerozoic at both family and generic level. The general decline in rates seen just in the Palaeozoic continues in the Meso-Cenozoic. However, there appears to be a 're-setting' of the rates trend at the Permo-Triassic boundary. This is particularly noticeable in origination rates, which decline sharply from the Cambrian to the Permian, but then increase markedly in the Triassic. From the

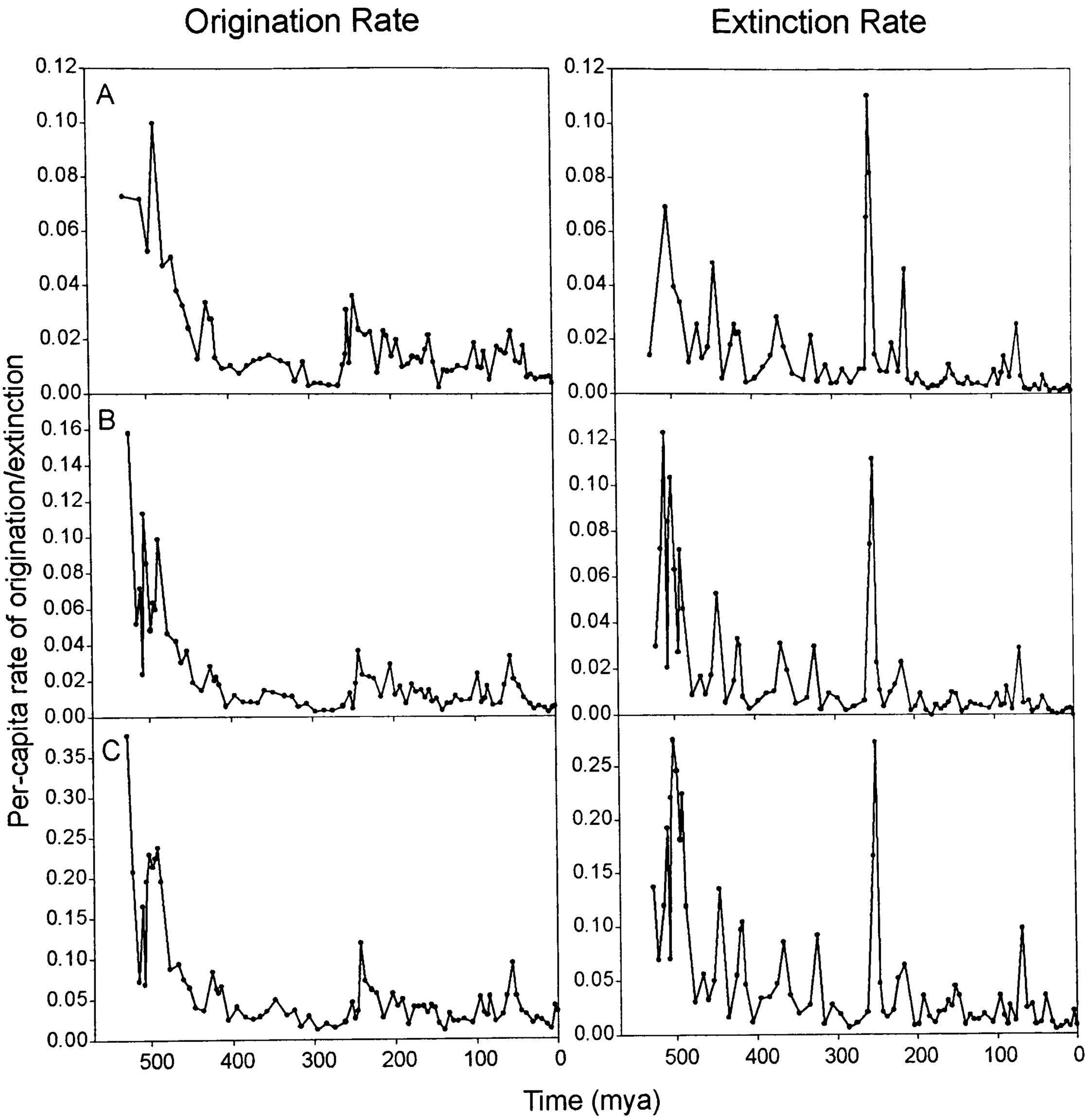


FIGURE 5.15. Per-capita rates of marine origination/extinction through the Phanerozoic. (A) Marine families. Data from Benton (1993) (B) Marine families. Data from Sepkoski (1992). (C) Marine genera. Data from Sepkoski (unpub.). Rates are in taxa per Lmy.

Triassic to the Recent only a very slight downwards trend is seen. Extinction rates also show a slight decline from Triassic to Recent, and their mean value remains lower than mean origination rate. As a result, diversification rate through the Meso-Cenozoic remains positive, and hence the very large diversity expansion seen in both families and genera through this time period is possible, even given declining origination rates.

5.3.2. Competitive displacement

5.3.2.1. Clade diagrams

The clade or 'spindle' diagrams representing the generic diversity of all 21 dominant invertebrate classes through the Phanerozoic are shown in Figure 5.16. Similar diagrams showing in detail only the Palaeozoic sections of the diversity histories are shown in Figure 5.17. The advantage of these diagrams is the ease of comparability they allow between the different classes. For example, Trilobita are shown to be by far the most dominant group in the Cambrian, although their maximum diversity is not achieved until the End-Ordovician. Similarly, Articulata are the most diverse class during the later Palaeozoic, although this dominance is diluted by the other members of the 'Palaeozoic fauna'. Figure 5.16 illustrates the dominance of the gastropods and bivalves in the Recent; their explosion in diversity, particularly that of Gastropoda, does not occur until after the K-T extinction. Compared to these two groups, the diversity contribution of other members of the 'modern fauna' appears negligible.

All clades display complex shapes of waxing and waning which are not easy to interpret in terms of potential candidates for competitive displacement. Two of the classes of the 'Palaeozoic fauna' (Cephalopoda and Stenolaemata) expand rapidly during the Ordovician and then remain at a steady diversity level until the Permian extinction, after which they re-diversify back to their Palaeozoic level, although this process is slower in the Stenolaemates. Crinoids expand at a more conservative pace and then fluctuate around a slowly increasing diversity level, before succumbing to the Permian extinction event, after which they do not recover their former diversity. Articulates have a similar pattern, although their diversity level in the Palaeozoic is much higher and the Permian crash in numbers much larger. It is not easy to say which, if any, of these varying patterns could be a candidate for competitive displacement. The most likely contender for one half of a potential 'double wedge' is the class Ostracoda,

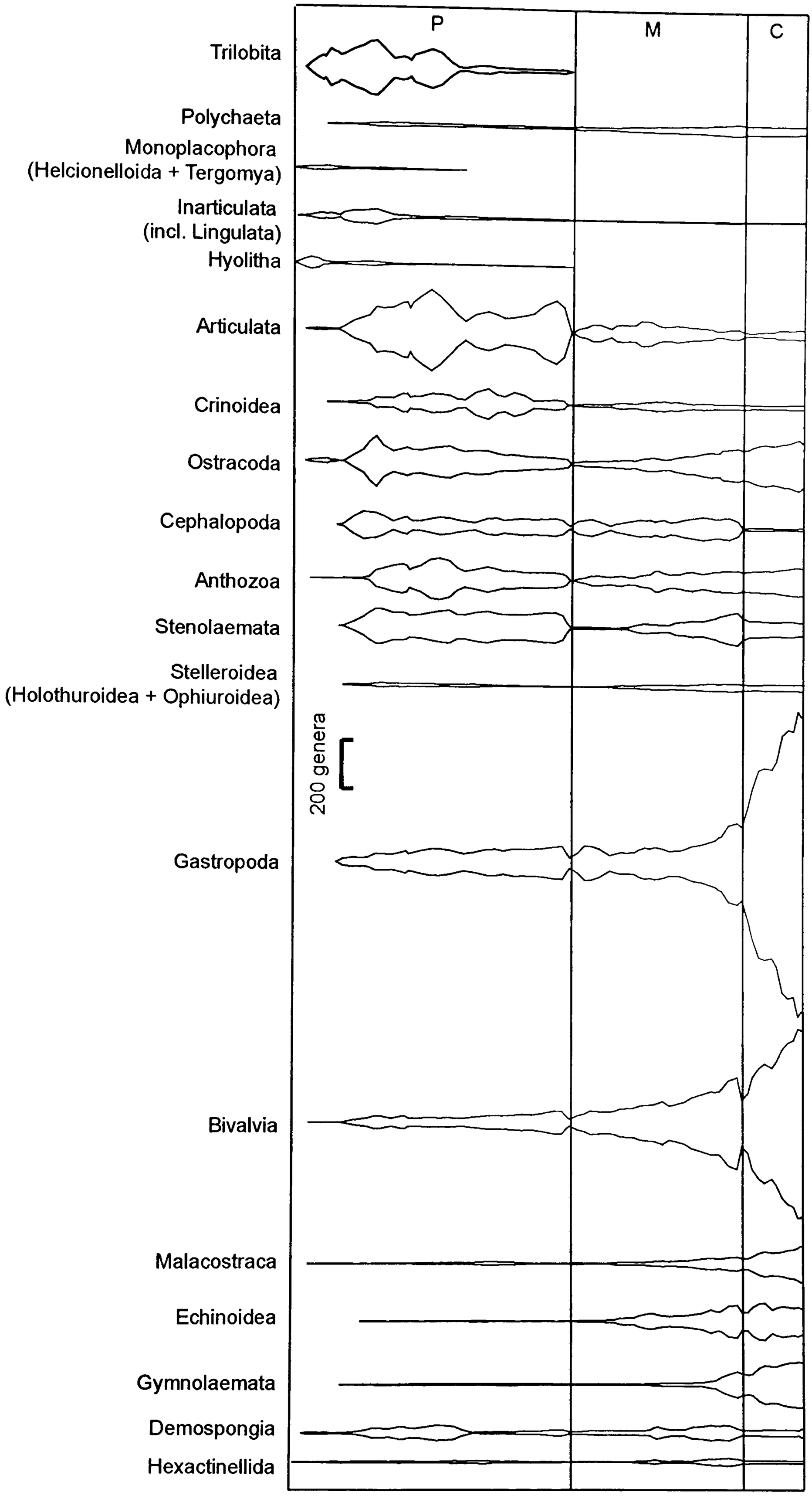


Figure 5.16. Generic diversity of the dominant invertebrate classes: Phanerozoic. The width of each clade diagram represents the number of fossil genera known to have been present within the class during each of 81 stratigraphic intervals. Data from Sepkoski (unpub.), M = Mesozoic, C = Cenozoic.

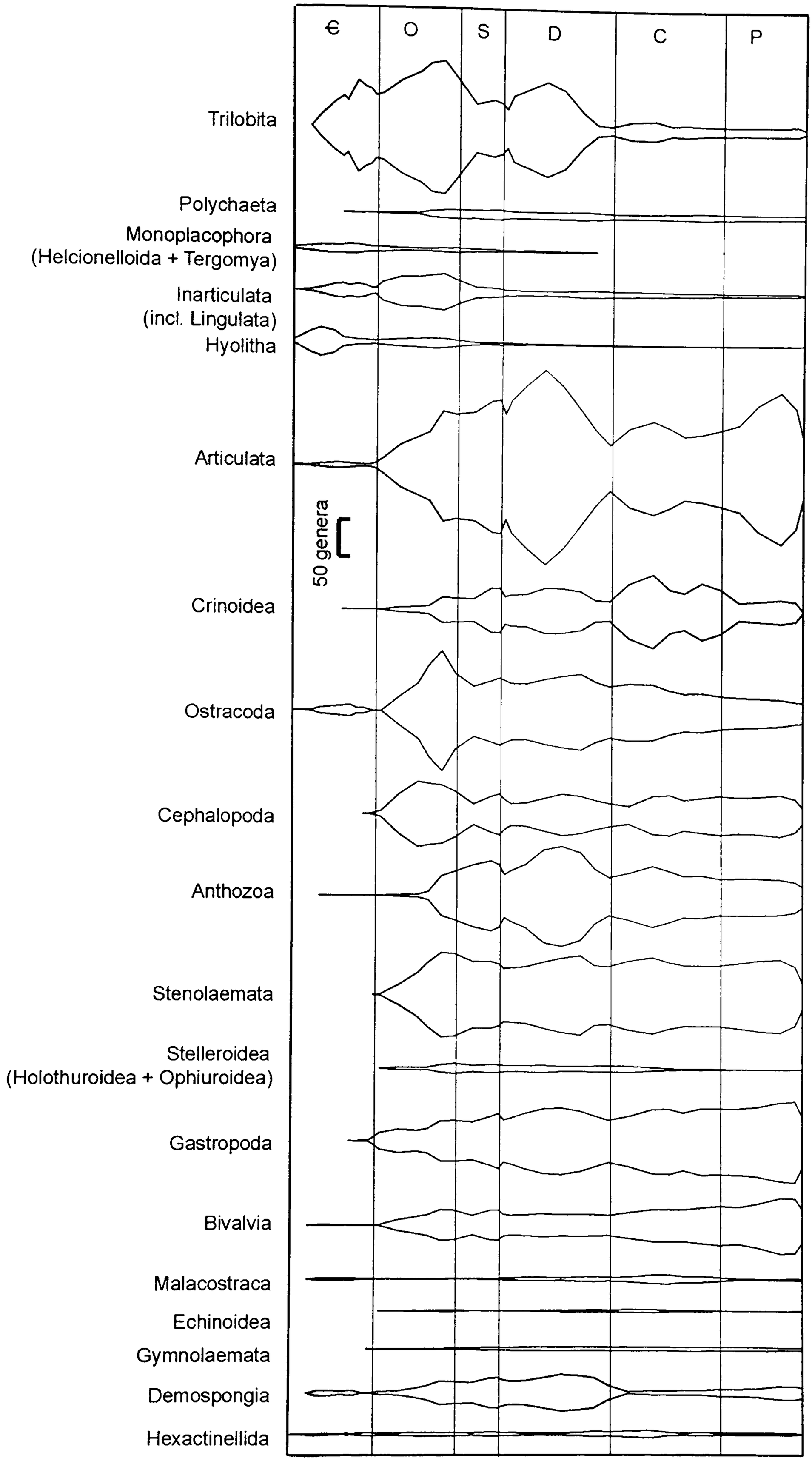


Figure 5.17. Generic diversity of the dominant invertebrate classes: Palaeozoic. The width of each clade diagram represents the number of fossil genera known to have been present within the class during each of 39 stratigraphic intervals. Data from Sepkoski (unpub.). Codes representing the Palaeozoic series are shown at the top.

which diversifies rapidly in the Ordovician, only to experience a continual gradual decline through the remainder of the Palaeozoic. However, a candidate for the other half of the double wedge is not obvious - of the Modern fauna only gastropods and bivalves are expanding as Ostracoda declines. In fact, Ostracoda re-diversifies after the End-Permian, reaching its diversity maximum in the Pliocene. In terms of the 'double wedge' model, this would indicate the removal or reduction of any competitors, certainly not the case for Bivalvia or Gastropoda. Anthozoa displays a similar pattern to Ostracoda. A further possibility for a candidate competitive displacement is Inarticulata versus Articulata, although only a limited number of the numerous articulate taxa could have been interacting with the much smaller inarticulate group.

In all cases, it is more likely that a combination of various taxa with similar ecologies but from a range of classes are competing, as opposed to a rigid taxonomic framework of one class versus another. From examination of the generic spindle diagrams presented here, the best candidates for a strictly taxonomic 'double-wedge' model remain the articulate brachiopods and the bivalves, two classes which do display a parallel waxing and waning of diversity similar to the hypothetical shapes illustrated in Figure 5.5, and at least some overlap of ecologies and geographic ranges.

5.3.2.2. An exponential model of bivalves vs. articulate brachiopods

The attempt to model bivalve and brachiopod diversification as an exponential growth curve, punctuated by mass extinction events, is illustrated in Fig. 5.18. Also included in this figure for comparison are the empirical diversity curves of the two classes, and Sepkoski's (1996a) model of the system using coupled logistic equations. Table 5.4 shows the real mean diversification rates of bivalves and brachiopods over the Phanerozoic, the rates used in the exponential model and the pre-equilibrium rates used in Sepkoski's logistic model.

	Diversification rate	
	Articulata	Bivalvia
Empirical data – mean over Phanerozoic (singletons excluded)	0.014	0.015
Exponential model	0.033	0.0205
Logistic model (Sepkoski 1996a)	0.060	0.030

Table 5.4. Real and model Phanerozoic diversification rates for Articulata and Bivalvia. Units in genera per Lmy.

The mean diversification rates of Bivalvia and Articulata are very similar over the Phanerozoic, and both are lower than the model rates used. However, the empirical averages include the negative diversification of mass extinctions, and the zero diversification of 'equilibrium periods'. The exponential model diversification rate is therefore higher than the empirical as it is exclusive of mass extinctions, which are modeled separately. The logistic model rate is exclusive of the End-Permian event and the two proposed equilibrium periods where diversification rate is reduced. Both models have a background diversification rate that is higher for brachiopods than for bivalves. However, total brachiopod diversity is kept lower than that of bivalves by differential response to mass extinctions in the case of the exponential model (Fig. 5.18B) and by a lower equilibrium diversity parameter in the case of the logistic model (Fig. 5.18C and Sepkoski 1996a, Table 9.2).

The form of the two exponential model curves is similar to the empirical patterns in terms of the large impact that mass extinctions have on both bivalve and brachiopod diversity. In addition, the general pattern of bivalve diversification (dotted line, Fig. 1.18A, B) is reasonably reproduced as an exponential curve punctuated with mass extinction events, although the level of diversity does become higher by the end of the Palaeozoic than that seen in the empirical data. Articulate brachiopod diversification is much more difficult to model using exponential growth. Despite the large drops in diversity brought about by the mass extinctions through the Palaeozoic, the modeled brachiopod diversity continues to show an overall rise through this period, rather than the fall evident in the real data. Similarly after the End-Permian event, at which articulate generic diversity was re-set almost to zero, the exponential model displays an

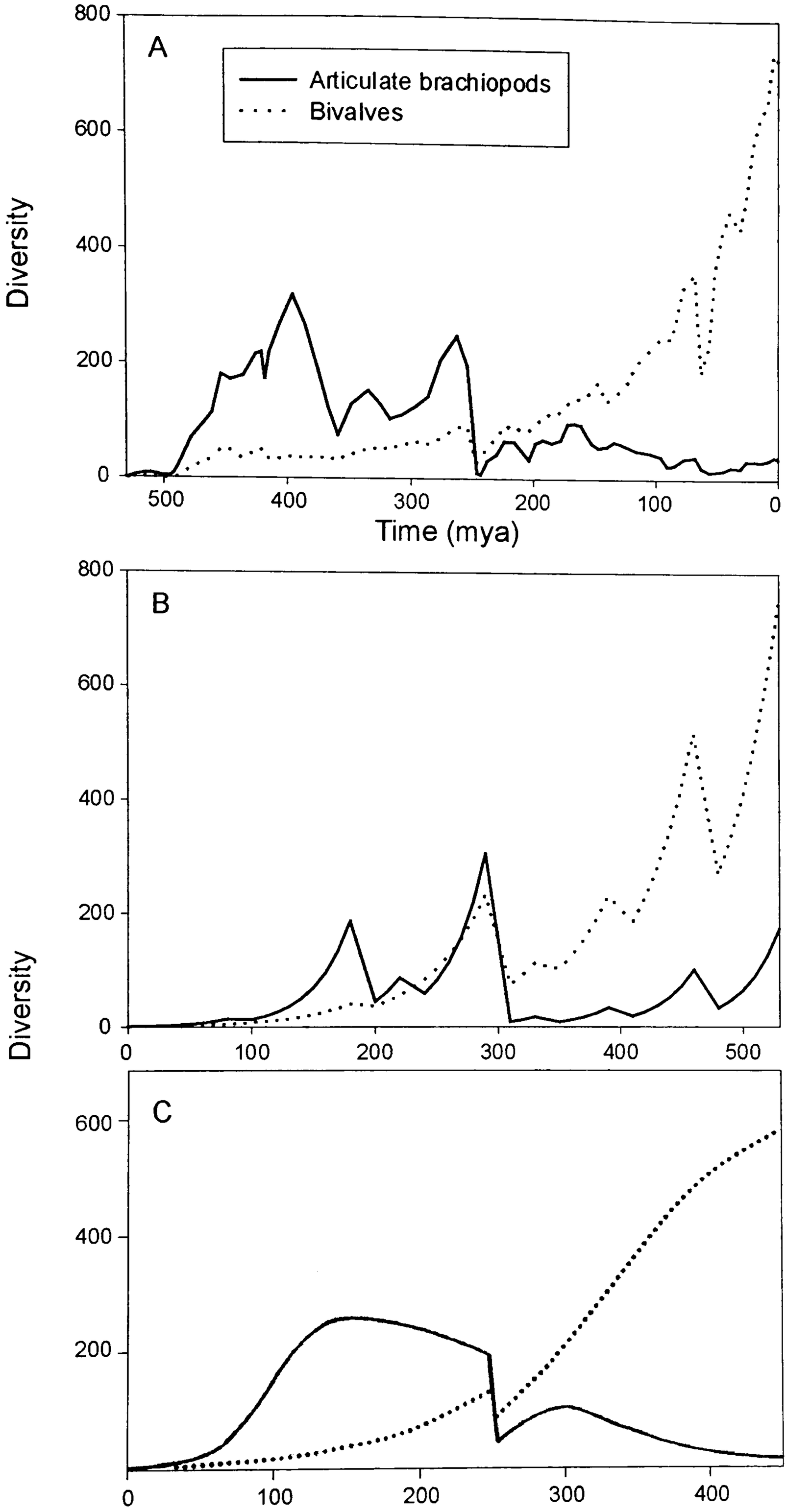


FIGURE 5.18. Empirical and model Palaeozoic diversity histories of bivalves and brachiopods. (A) Generic diversity. Data from Sepkoski (unpub.). (B) Modelled diversity - exponential diversification with multiple mass extinctions. No interaction implied between the two clades. (C) Modeled diversity - Logistic diversification with End-Permian mass extinction (from Sepkoski 1996, Fig. 9.15). Interaction between the two clades is implied.

expansion to the Recent, albeit with large drops, and not the expansion and then decline that brachiopods display.

Conversely, the logistic model does mimic these trends in brachiopod diversity suggesting that it is a better model for the growth of this clade than the exponential. However, the logistic decline in diversification modeled for bivalves in the Cenozoic, leading to an equilibrium of 600 bivalve genera in the near future, is not evident in the empirical data which have already exceeded this level of diversity (Fig 5.18A). The overall form of the bivalve curve appears strongly exponential.

The general trends in diversification and turnover rates for both bivalves and articulate brachiopods are shown in Figures 5.19 and 5.20. Diversification rates for both through the Phanerozoic fluctuate around a positive value (Fig. 5.19), but brachiopods display far larger deviations from the trend at mass extinction events. Turnover in both groups reduces from the Ordovician to the Recent (Fig 5.20), although there seems to be a decoupling of the patterns before and after the Permian extinction event. Turnover in articulates is in general significantly higher than that in bivalves, indicating that this is a more volatile group in evolutionary terms.

5.4. Discussion

Significance of evolutionary rates

The results of the analysis of evolutionary rates through the Palaeozoic diversity expansion to the 'equilibrium' period presented here, confirm those of previous studies (Sepkoski 1978, 1979; Alroy 1998; although see Foote 2000), specifically that origination rates display diversity-dependent behaviour, but extinction rates do not. Origination rates have declined through the Phanerozoic as diversity has increased, although there is large variation around the mean trend (Sepkoski 1998b). This trend seems to be 're-set' at the Permian extinction event – there is a downward trajectory through the Palaeozoic, but after the Permian depletion of taxa, origination rate increases rapidly in the early Triassic and then declines once more (Fig. 5.15; Sepkoski 1998b, Fig. 1). Several reasons for declining extinction rates have been suggested previously. Gilinsky and Bambach (1987) proposed a variant of the Red Queen hypothesis (Van Valen 1973): basic adaptations of successful groups are established early in their history, but when a group's biotic context changes due to turnover in surrounding taxa, initial adaptations become less advantageous and speciation rate

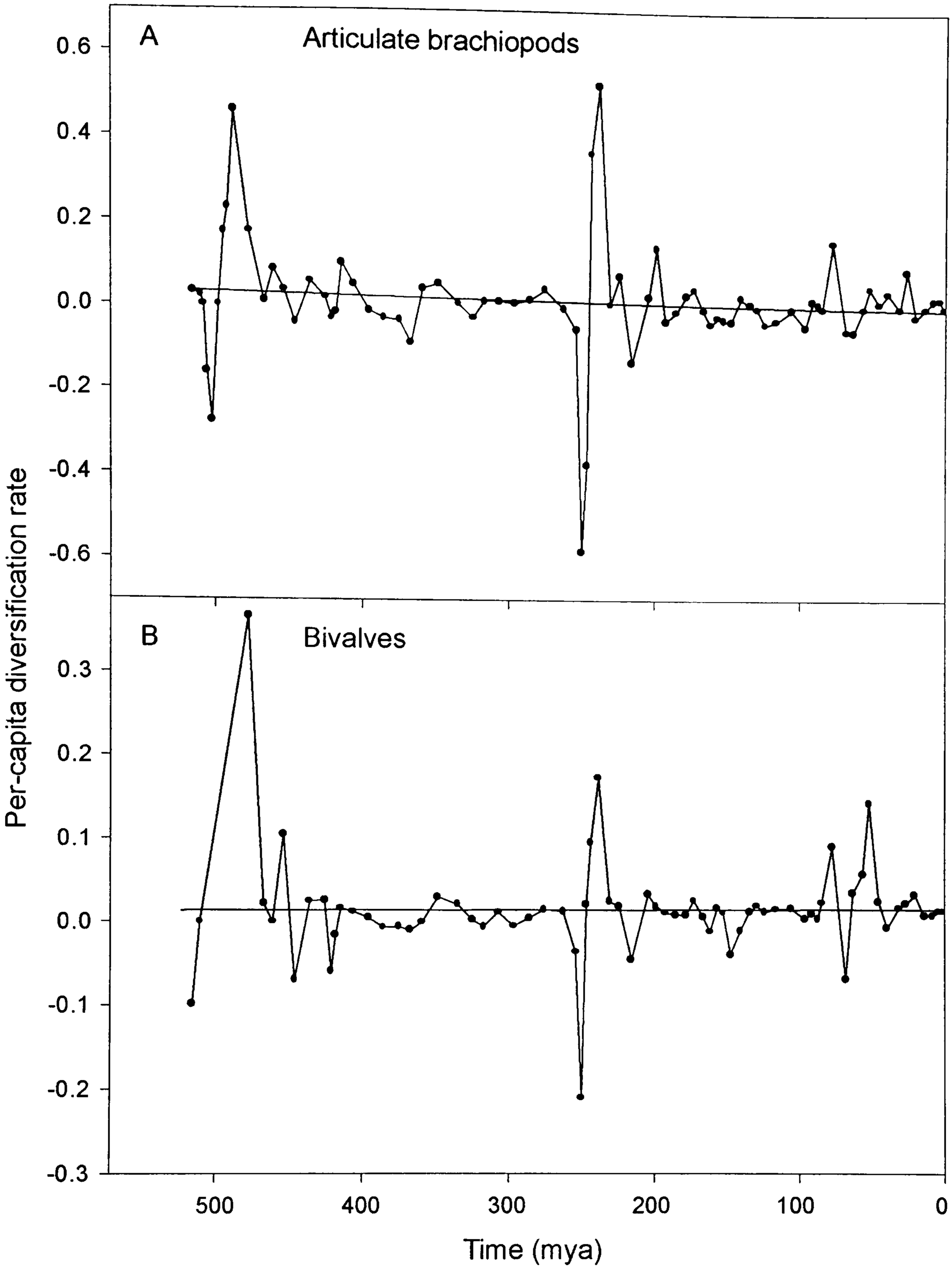


FIGURE 5.19. Brachiopod and bivalve per-capita diversification rates through the Phanerozoic. (A) Articulate brachiopod genera. (B) Bivalvia genera. Data are from Sepkoski (unpub.). Rate units are taxa per Lmy. Least-squares linear trend lines are shown.

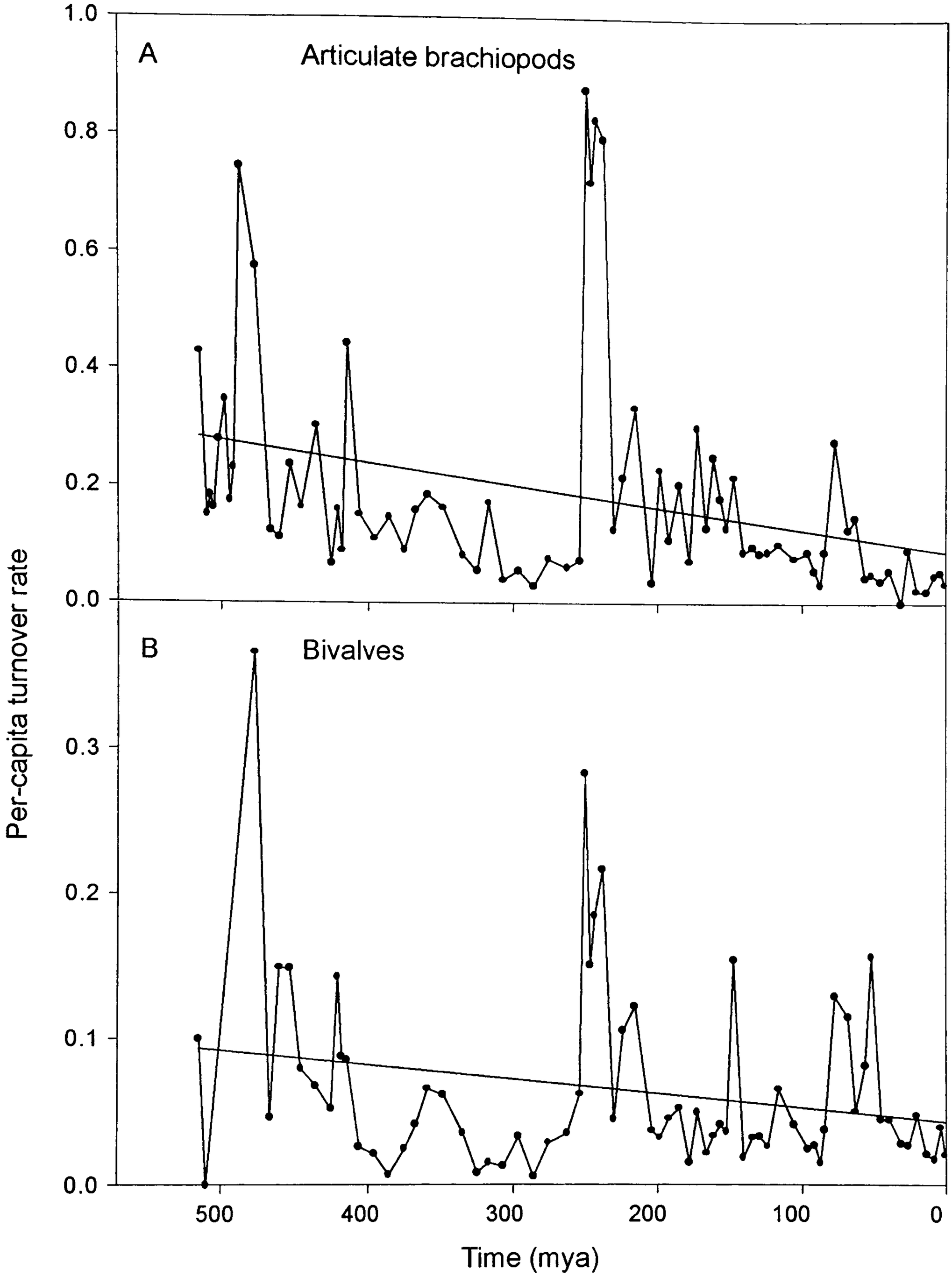


FIGURE 5.20. Brachiopod and bivalve per-capita turnover rates through the Phanerozoic. (A) Articulate brachiopod genera. (B) Bivalve genera. Data are from Sepkoski (unpub.). Units are taxa per Lmy. Least-squares linear trend lines are shown.

declines. Alternatively they suggest that genetic and developmental systems may become resistant to change as they age. Sepkoski (1998b) advocates a third, diversity-dependent alternative - the crowding effect of a radiating group, filling niches and decreasing further speciation. The reduction in origination rates taken in isolation does suggest some kind of 'crowding' control on the number of taxa in existence. However, extinction rates also decline through the Phanerozoic (Fig. 5.15; Gilinsky 1994; Newman and Eble 1999). Exponential or expansive diversification can occur through the Phanerozoic even given falling origination rates, if extinction rates reduce in tandem. It is the difference between the two, the diversification rate, that determines the form of diversity increase. This difference is on average positive through the Meso-Cenozoic, hence the large expansion of marine and continental organisms since the Triassic is possible despite the general trend of a reduction in origination rate.

The pattern in the Palaeozoic alone is different from that in the Phanerozoic as a whole. Generic diversity increases during the Cambro-Ordovician radiation, but diversification after this is on average negative, resulting in the gentle decline of diversity from the Mid-Ordovician to the Permian (Fig. 5.12A). The Palaeozoic era is characterised by:

- Declining origination rate
- Weakly declining extinction rate
- Reduction of turnover
- Increasing taxonomic longevity
- Movement of diversification rate towards zero.

Hence, the 'dynamic equilibrium' of the Palaeozoic plateau would appear to be not so dynamic. Instead of an increase in extinctions as competitive interaction escalates, the diversity system of the later Palaeozoic actually becomes more stable, less dynamic and the taxa more immune to extinctions as diversity increases and then levels out. This is in contrast to the Cambrian period, where mean taxonomic longevity is short, and extinction and origination rate much higher, suggesting a system in flux with a high level of turnover. This pattern corresponds to one of Boucot's *Ecologic Evolutionary Units* (EEUs), time units through the Phanerozoic characterised by biotic associations involving different community groups (Boucot 1983, see also Sheehan 1996). Each EEU begins with a brief period of reorganisation and concludes with a global extinction

event. There are two possible reasons for this change through the Palaeozoic: (1) external perturbations become less frequent, reducing the chances of random extinctions; and (2) the taxa themselves become less extinction prone and more able to survive environmental perturbations, or invasions of competing taxa. It could be that extinction rate declines as a consequence of declining origination rate, as there are fewer new taxa exerting competitive pressure. However, as Figures 5.13D and 5.14D show, the correlation between contemporaneous origination and extinction rates is little better than that seen in a stochastically generated diversity system, suggesting that originations do not drive extinctions.

Kirchner and Weil (2000a) investigated this question for marine per-taxon evolutionary rates through the Phanerozoic, and found a correlation between extinction rates, and origination rates 10 million years later. Some support for such a lag period is given by the stronger correlation between extinction rates and origination rates from two stratigraphic intervals later, than is evident between contemporaneous rates (Figs. 5.13D, E), which leads to the hypothesis that, to a certain degree, originations are reacting to extinction events. While extinction and originations display some level of lagged-correlation, they appear to be independent of standing diversity level over the plateau period, and are therefore stochastic with regards to diversity. Indeed, extinction rate data are generally noisy, and as there is some evidence that they precede originations, it can be concluded that the majority of these events are random environmental perturbations and not biologically driven. This suggests that the mechanism of replacement of one taxon by another through the Palaeozoic plateau period is closest to Benton's 'double-wedge' types 2 - 4 (Benton 1996 and Fig. 5.4), where mass-extinction is involved, and new taxa can become established only after the chance extinction of 'incumbents' (Rosenzweig and McCord 1991). A similar finding using species data was reached by Emilliani (1982) which he termed "extinctive evolution". This conforms to Kitchell and Carr's (1985) suggestion that there is an asymmetry to the response of diversity to environmental perturbations – an abrupt diversity decline is followed by a relatively slow recovery. However, the correlation between both contemporaneous and lagged rates is fairly weak ($R^2 = 0.22$ and 0.37 respectively), the level of organisation in the data is little better than between the rates of a randomly generated phylogeny. Hence, the majority of originations are independent of extinctions as well as standing diversity, following type 5 of Benton's double wedge models (Benton 1996 and Fig. 5.4), the 'stochastic broom' hypothesis.

From this accumulated evidence a synopsis of marine diversification through the Palaeozoic can be constructed. Extinction rate is largely diversity independent, and extinction events are generally random, probably driven by environmental perturbations, and not a direct result of origination events – only a weak negative correlation is found between extinction rates and diversity. Origination rate is diversity dependent during the initial radiation and leveling out of the plateau - it is significantly higher during the low diversities of the Cambrian than in the later highs of the Silurian-Carboniferous. Hence diversification is deterministic during the course of the Cambro-Ordovician radiations. This situation changes over the period of diversity stasis itself, with origination rate becoming diversity independent. Extinction and origination rate are weakly correlated with a two interval time lag of originations. Therefore, to a limited extent extinction events produce origination events. However, this correlation is weak: in general both origination and extinction rates over the plateau period display stochastic behaviour. Hence this analysis finds little evidence for an ecologically controlled deterministic equilibrium.

Articulate brachiopod displacement by bivalves

The results of modeling the brachiopod-bivalve diversity system as a pair of decoupled exponential growth equations are equivocal. The pattern of bivalve generic diversification can be readily mimicked by an exponential curve interrupted by mass extinction events, indeed a log plot of the empirical data is fit well by a linear growth line (Benton 2000). Hence, the diversification pattern of bivalves appears to be one of expansion, although this does not preclude some reduction of the diversification rate caused by competitive interactions. Conversely it has proved impossible to reproduce the diversification pattern of articulate brachiopods adequately in the same way. Despite the large depletion effects of mass extinction events, the diversity levels of the modeled system increase beyond those seen in the empirical data. It is concluded therefore, that either brachiopod diversification was wholly or mainly stochastic in nature, with little more propensity for originations than for extinctions, or that there was some limiting factor imposed upon it. Competitive displacement of articulates is a possibility, but there is no evidence from the diversification pattern of bivalves that they are responsible. Sepkoski (1996a) reproduced the pattern of bivalve diversification using a logistic growth equation, but unlike that of the articulates, his curve for bivalves predominantly consisted of the initial expansive phase of the logistic, with only slight

signs of leveling out towards the closing stages. The empirical data curve for bivalve generic diversity shows no signs of an equilibrium being achieved in the near future. In addition, the ecological case for interaction of bivalves and articulate brachiopods is not compelling. It is probable that only epifaunal bivalves share feeding strategies with the articulates, hence it is not clear that infaunal taxa should be included in any proposed competitive interaction (Sepkoski 1996a). Also, it was only towards the end of the Palaeozoic era that the habitat ranges of the two classes overlapped to any significant degree, when bivalves spread into the middle to outer-shelf environments favoured by the brachiopods (Miller 1988). Generally, bivalve taxa were most diverse and abundant in near-shore settings (Gould and Calloway 1980). If the brachiopods suffered competitive displacement from the Late Palaeozoic onwards it is more probable that this was a result of interaction with a less easily defined group of ecologically similar, but taxonomically disparate organisms, than those represented by class Bivalvia. It is also likely, especially in shallow water habitats, that environmental disturbance is important in reducing the scope for inter-specific competition, with the primary cause of mortality being factors such as predation and disturbance rather than competitive pressure.

5.5. Conclusions

- Evolutionary dynamics through the Palaeozoic era are characterised by declining origination and extinction rates, a reduction in turnover and an increase in taxonomic longevity.
- Extinction rates through the Palaeozoic display only a weak negative diversity-dependence. It is probable that extinctions are predominantly random events.
- Origination rates are correlated negatively with standing diversity from the Cambrian diversity low, through the Cambro-Ordovician, and rise to the subsequently higher diversity levels of the later Palaeozoic. Therefore origination rate is diversity-dependent during the radiation.
- Conversely, origination rate is diversity-independent during the Palaeozoic diversity plateau itself.
- There is no evidence for the negative correlation between origination and extinction rates predicted by the logistic model through the plateau period, and

hence no evidence that the Palaeozoic plateau is an ecologically determined structure.

- There is a weak correlation between extinction rate and origination rate, with a lag of two stratigraphic intervals. This provides some evidence that, to a limited extent, extinction events allowed subsequent origination events to take place. However, the behaviour of origination and extinction rates through the plateau period is primarily stochastic in nature.
- The following hypothesis of diversification through the Palaeozoic era is proposed: Origination rate-driven, deterministic growth during the Late Cambrian and Ordovician, followed by stochastic diversity dynamics during the remainder of the Palaeozoic until the End-Permian extinction event.
- Articulate brachiopod diversification cannot be modeled as exponential, implying some limiting factors on diversity levels of this class. Some degree of competitive displacement is probable, but it is unlikely to be predominantly due to competition with bivalves, which display an expansive growth pattern with no evidence of interaction.

CHAPTER 6. DISCUSSION

The research presented here investigates a number of issues concerning the nature of biodiversity estimates, and patterns of diversity change and turnover rates evident in global taxonomic data for the Palaeozoic era. The following discussion attempts to draw together the various results and conclusions of these analyses, and to evaluate their implications for our understanding of the diversification dynamics of early Phanerozoic marine life.

6.1. Enhancing biodiversity estimates

The use of ghost lineages to enhance biodiversity estimates has been advocated in a number of studies (Smith 1988; Norell 1992, 1993; Norell & Novacek 1992a, 1992b). These analyses made the assumption that phylogenetically corrected counts are superior to those provided by raw taxonomic data, without testing one method against the other and comparing them to the real pattern. Here, such a test was applied to simulated phylogenies, and the phylogenetic method proved superior to the taxic at capturing patterns of lineage diversity in the majority of diversification scenarios, particularly those involving large clades with many extant representatives. However, the corrected patterns are skewed in certain situations. Where ancestral taxa are misdiagnosed as the sister taxa of their descendent groups, diversity counts are artificially inflated. The phylogenetic method also magnifies the Signor-Lipps sampling artefact seen before mass extinction events, and at the end of diversity study periods – artefacts also described as edge-effects (Foote 2000a). Hence, the phylogenetic method of enhancing diversity estimates is considered to be inappropriate for studies of extinct clades, particularly those containing relatively few taxa or suffering many large extinction events. In these situations the phylogenetic estimate reduces diversity counts artificially towards the end of the history of a clade, resulting in a skewed pattern with the clade appearing more diverse in early intervals. The phylogenetic estimate is not feasible for studies of long-term global diversification due to the lack of complete information regarding the phylogenetic relationships of the taxa involved. If the method were to be used to construct Palaeozoic marine diversity patterns, such as those considered here, it is predicted that the Palaeozoic mass extinction events would be smeared backwards in time. This effect would distort the End-Permian event to such a degree that

diversification during the latter half of the era would follow a downwards trend, following a diversity maximum during the Mid-Ordovician. Due to the perceived inadequacies of raw taxonomic range data, the use of correction methods such as the phylogenetic estimate are increasingly advocated (Smith 1994, 1988; Norell 1992, 1993; Norell & Novacek 1992a, 1992b). The results presented here demonstrate the need for rigorous tests with simulated data, to identify situations where the method is inadequate or provides erroneous results, before empirical patterns are altered and raw data curves abandoned.

The analyses of Palaeozoic diversity patterns conducted here used un-enhanced counts. Adjustments were only made to the extent of removing uncertain taxonomic range assignments and single interval taxa. The use of raw data from global fossil-range compendia has been criticised (e.g. Hoffman 1985, 1988; Patterson and Smith 1987, 1989; Boucot 1990; Smith 1994) but its application can be justified as follows:

- The research presented here demonstrates our current 'state-of-knowledge' of Palaeozoic biodiversity patterns. Such a comprehensive review is desirable, firstly to clarify the situation as we currently understand it, providing evidence for the various hypotheses of Palaeozoic diversification, and secondly as a basis for comparison with any future enhanced results.
- As the tests of the phylogenetic estimate prove, enhancement methods introduce unforeseen errors and skew of their own, in addition to that within the raw data. Such methods must be comprehensively tested before the patterns that they recover can be considered as 'more correct' than those yielded by traditional taxonomic range data.
- Many enhancement methods, e.g. the phylogenetic estimate (Norell 1992, 1993), and sampling standardisation (Alroy 1999, 2000), cannot be applied to the currently available global compendia of first and last appearance data. Much further research effort is required to make available the data required for the application of these methods to global diversity patterns. As an example, the *Paleobiology database* under construction at the National Center for Ecological Analysis and Synthesis in California, for use with sampling standardisation techniques, currently includes adequate coverage to produce global diversity curves for five marine classes during the Mid-Ordovician to Carboniferous, and

the Late Jurassic to Paleogene only within limited geographical locations (Alroy et al. 2001).

Hence, use of the latest large compendia of fossil-range data is currently the only direct way to assess global Phanerozoic diversity patterns, and to provide an analysis as comprehensive as that presented here.

6.2. The nature of the Palaeozoic plateau

Due to the lack of global species fossil-range data, the suggestion of Benton (1995, 1997, 2001) that the Palaeozoic plateau may be an artefact of taxonomic level has not been tested satisfactorily. However, the analysis presented here shows that a period of apparent diversity stasis from the Mid-Ordovician to the Mid-Permian is a robust feature of diversity curves at ordinal, familial and generic taxonomic levels, and that the logistic model, including an extended period of diversity equilibrium, fits the form of the Palaeozoic curves well. This research also shows that the importance of the plateau as a dominant feature of the curve diminishes as the ranks of the Linnaean hierarchy are descended; this is due principally to the relative increase in Meso-Cenozoic diversity at lower levels in the taxonomic hierarchy. The model of species diversification, constructed by extrapolation of the trends evident from familial to generic level, suggests that this rise, and hence the degradation of the plateau, is even more pronounced in species data. In the species model the Post-Permian increase is large enough to reduce the logistic elements of the marine curve to the extent that the overall form of diversity increase appears exponential. Debate continues over the significance of the Meso-Cenozoic radiation. At least some of the Cenozoic taxonomic increase is likely to be due to the 'Pull of the Recent' phenomenon (Raup 1979a; Sepkoski 1997). The rise could also be an artefact of increasingly poor sampling back through the Phanerozoic (Raup 1972), yielding a pattern of Cambro-Ordovician expansion followed by little subsequent increase (Alroy et al. 2001). A study investigating the quality of the fossil record through time as assessed by congruence between cladogram shape and sequence of fossils in the rocks has refuted the idea that the fossil record becomes increasingly poor with age (Benton et al. 2000), and asserts that it is adequate to capture the large-scale patterns of first and last appearance times of fossil higher taxa on a global scale. It is also probable that the long term diversity signal

as illustrated by raw data curves is too strong to be accounted for entirely by the decreasing amount of preserved rock in increasingly older intervals of the Phanerozoic (Foote 2002 pers. com.). The "Pull of the Recent" artefact is also not enough to explain the resetting of turnover rates seen at the P-T boundary.

Having established that the Palaeozoic plateau is a consistent feature of global marine diversity curves, at least to generic level, we come to the question of its ecological significance. The results of the stochastic phylogeny simulations presented in Chapter 4 indicate that a diversity equilibrium period could have arisen by chance. However, such a plateau following a large taxonomic radiation early in the history of a diversification system, such as that in the Ordovician, is much harder to reproduce stochastically. These results are corroborated by the tests for diversity-dependence of turnover rates during the Palaeozoic. Origination rate is diversity-dependent from the period of diversity low in the Mid-Cambrian, through the Ordovician radiations, to the diversity highs of the plateau. The rate of appearance of new taxa decreases with increasing diversity. This may reflect the filling of ecological niches, and an increase in crowding effects and inter-taxonomic competition. It could also be explained, however, by the gradual replacement of taxa with a high speciation rate by those with a more conservative rate of speciation. Throughout the plateau period both origination and extinction rates are diversity-independent, apparently fluctuating randomly in a manner similar to that evident in the stochastic simulations. Hence, it is concluded that the Ordovician radiations are driven deterministically by origination rate, while the plateau is characterised by underlying origination and extinction rates that are random in their behaviour. The interpretation of the plateau falls into category (2) of those proposed in Chapter 1 (Section 1.4.1): The plateau is real, but is a stochastic structure. This is the *neutral model* of Hoffman (1986, 1986) which assumes random rates of origination and extinction. No ecological or biologically determined constraints are implied, and the apparent equilibrium with fluctuations is simply a random element in the growth pattern of diversity.

Can we explain this change from deterministic to stochastic diversification behaviour from an ecological perspective? It would seem that opportunities for new taxa to originate became more scarce as the Ordovician progressed, as the number of niches available for exploitation diminished. Interestingly, extinction rate over the same period was not diversity-dependent as predicted by the logistic model, but shows a slight downward trend as diversity increased. Hence, the filling of niches and predicted

increase in competition did not cause an increase in extinctions – such events appear to be generally random. Once the Ordovician radiations slowed and ceased, the 'steam' seems to have gone out of the diversity system of the Palaeozoic. The plateau period is characterised by high taxonomic longevity, and low and randomly fluctuating rates of origination and extinction. Bambach (1985) identified a strong link between change in diversity and change in adaptive variety of the constituent taxa. From the evidence presented here we can speculate about the relationship between the ecological characteristics and the changing diversification dynamics of taxa through the Palaeozoic.

The Cambrian and early Ordovician periods were characterised by taxa with a high innate rate of speciation, and a low extinction resistance. These taxa are analogous to the *r* strategists of population ecology which thrive in unstable environments; they invest heavily in reproduction (a high *r*-value), have a variable mortality rate dependent on environmental fluctuations, and tend to be opportunists (Begon et al. 1996). Evolutionary *r* strategists, with high rates of origination and low longevity, dominated the unstable diversity system created by the empty ecospace of the Cambrian, a time of sudden appearance of new body plans. Carroll (2001) is the most recent to note that diversity radiations are associated with the appearance of key morphological or physiological traits, which allow the surmounting of a previous constraint. He identified these periods as the result of active, directional trends within the overall passive arc of evolutionary history. As the diversity system matured through the Ordovician and into the plateau period itself, short-lived 'pioneer' taxa evolved into those with a much lower innate rate of origination and a higher resistance to environmental perturbations, producing greater longevity – evolutionary *K* strategists. *K* strategists in population ecology are taxa with low reproduction rates which invest heavily in increased survival, make a large proportional contribution to a stable population level (*K*), and are the products of stable and mature ecosystems (Begon et al. 1996). This analogy not entirely accurate, however, as the simplest definitions of *K* strategists include the ability to thrive under conditions of high inter-species competition (Begon et al. 1996). The density-independent origination and extinction rates through the Palaeozoic indicate that macroevolutionary inter-taxon competition was not a determining factor of the marine diversity system at this time. Kuno (1991) rejected the *K* strategists concept, and suggested that a more reasonable defining characteristic of species populations is their susceptibility to crowding – the likelihood that they will be excluded by inter-species

competition. Applying this definition to the macroevolutionary system of the later Palaeozoic reveals taxa that were characterised by a low susceptibility to crowding, with origination and extinction random with respect to diversity level, rather than the products of inter-taxonomic competition. Application of the *r/K* strategists model to evolutionary scenarios is not entirely productive as the analogy between speciation rate and reproductive rate is not accurate. A high or low reproductive rate may be an evolutionary adaptation of a species, but a clade's speciation rate cannot be seen as such.

The Mid-Late Palaeozoic taxa displayed a wide variety of life-habit adaptations, which evolved during the Ordovician radiations and became established through the remainder of the era. These modes of life included colonial growth forms (Anthozoa, Bryozoa, Graptolithina), morphologies allowing survival on different substrates (Articulata, Bivalvia, Gastropoda, Ostracoda), erect forms with efficient filtration fans (Crinoidea), and active nektonic predators (Cephalopoda) (Bambach 1985). From the Mid-Ordovician onwards, when these life strategies became established, the marine ecosystem of the Palaeozoic can be imagined as one of relative stability, punctuated only occasionally by turnover and extinction, similar to that envisaged for many ancient communities (Conway Morris 1998). Such community stability has become formularised in the concept of *coordinated stasis* (see Bambach and Bennington 1996), and may be produced not as a result of dynamic equilibrium governed by competitively driven originations and extinctions, but as the end-product of a maturing ecosystem following a period of biotic turbulence. Under this scenario the plateau itself is the diversity expression of a marine community containing an abundance of taxa with highly adapted life strategies, a low tendency for further innovation, and a low susceptibility to crowding. The relatively few originations and extinctions are predominantly random with respect to diversity. Such a period is perhaps characterised by a 'passive evolutionary trend' (Carroll 2001). In the absence of diversity-dependent rates there is no evidence supporting the concept of a global carrying-capacity predetermining an upper limit to Palaeozoic diversity. The decimation of the long-lived Palaeozoic taxa at the end-Permian extinction event re-set the evolutionary clock (Bambach 1985). *r* strategists once again became abundant, and deterministic origination rate-driven diversification resumed, resulting in an increase in modes of life little seen during the Palaeozoic, such as the major expansion of infaunal life-habits (Thayer 1983) and of predatory feeding strategies (Vermeij 1977). There is no reason to

assume that such periods of active innovation are becoming rarer – the acceleration of diversification in the Cenozoic suggests the opposite. This leads to the question as to why a slowing of innovation is evident in the Palaeozoic, if it is not indeed simply a stochastic effect. This requires further investigation.

The reality of macroevolutionary inter-taxonomic competitive displacement has been addressed briefly here, in an attempt to model the purported patterns of long-term interaction between bivalves and articulate brachiopods as two independent exponential curves. The results, as in prior studies, do not provide a conclusive answer. Bivalve diversification has been modeled as both a logistic increase (Miller and Sepkoski 1988; Sepkoski 1996a) and an exponential growth curve (Benton 2001). There is little to distinguish between these two variants – both models allow for the possibility of competitive 'damping' of the growth rate of bivalves, and both models fit the empirical data well. The difference is that the logistic model predicts bivalve diversity will eventually reach a plateau as a result of inter-taxonomic competition. The exponential model makes no such prediction, assuming that while competition may lower the rate bivalve diversification, it will not halt it entirely. The exponential model incorporating mass extinctions presented here mimics the real curve of bivalve diversification well (Fig. 5.18). There is no requirement for the extra 'damping' parameter of the logistic equation, and the loss of significance that this produces. Parameters added to a model to amplify its goodness-of-fit increase the resulting correlation coefficient, but decrease its significance (Walker 1985).

This is not to say that competitive interactions do not affect bivalve diversification. The diversification parameter of the exponential model used here is lower than the initial diversification value used by Sepkoski (1996a) in his logistic model of bivalve growth. This lower rate could be a product of competitive interactions among bivalves and other marine taxa, but this can only be speculation without knowing the unfettered rate of bivalve diversification in the absence of competitors. The exponential model implies no equilibrium to bivalve taxon numbers and no such equilibrium is evident in the bivalve curve. Any competitive pressure slows their growth curve, but does not impose an upper limit on their numbers. Conversely, articulate brachiopods do show an equilibrium, followed by a decline in numbers through the Meso-Cenozoic. Here, exponential modeling is not realistic, and a pattern predicted by competitive displacement is evident, although the end result of complete exclusion of the articulates is not achieved. It has been speculated that competition with bivalves

may be the mechanism determining this pattern (Miller and Sepkoski 1988; Sepkoski 1996a), but there is nothing in the exponential growth pattern of bivalves to suggest that specifically they were displacing articulate taxa. It is more likely that any pressure limiting and then reducing brachiopod diversification was the result of competition with a more diffuse ecological grouping rather than a strictly taxonomic one. As noted by Skelton et al. (1997) examination of biotic turnover patterns alone is not enough to test hypothesis of competition between organisms, as these patterns may be caused by many factors. While the limited modeling experiment does not disprove the theory of macroevolutionary competitive displacement, it confirms that evidence beyond simply the exponential diversification pattern of such groups as the bivalves, or the Modern evolutionary fauna, is required to prove that these groups of organisms brought about the large scale displacement of Palaeozoic marine life.

The discussion and conclusions set out here are specific to the Palaeozoic plateau. However, they have a wider significance for the current research effort seeking to construct general laws governing ancient and modern biodiversity change. Many events in the history of life – radiations, equilibrium periods, mass extinctions – invite generalised, deterministic hypotheses, even though they may result from a variety of independent causes, their coincidence in time due to chance and well within the expectations of an appropriate stochastic model (Raup et al 1973). We should not be too eager to formulate models with inherent causal mechanisms based simply on looking at a pattern of biodiversification, without first understanding which elements of the pattern are deterministic, and therefore in need of such explanations, and which display stochastic behaviour resulting from a myriad of unconnected individual origination and extinction events.

6.3. Future work

The accurate recovery of global Phanerozoic diversity patterns is an area of major ongoing research, with much emphasis on the increase, improvement and refinement of data. This includes the development of information technology and communications facilities. For example, recent publications have called for the increased use of the internet for the storage and access of global biodiversity databases (Knapp et al. 2002) and as an administrative base for international taxonomy (Godfray 2002). Avenues of future investigation specific to the issues raised here are suggested below.

- Additional simulations testing the phylogenetic method of estimating biodiversity, with a focus on mass extinction events. Statistical comparison of estimates with real diversity patterns over periods of sudden diversity decrease may uncover further inadequacies of the phylogenetic method at capturing these events. Further simulations incorporating realistic error rates into the simulated phylogenetic reconstructions will also highlight the potential problem of using poorly constrained phylogenies to calculate ghost ranges.
- Detailed analysis of diversity radiations. Sepkoski and Miller (1998) cited the periods of diversity rebound following mass extinction events as important evidence for the logistic model, claiming that they illustrate the proliferation of taxa in the absence of competitors. This could also be explained in terms of an exponential model with a varying diversification rate parameter.
- Modifications to the basic exponential model of diversification. Models need to be developed that allow for a changing r_d parameter within a system of exponential increase. This would cover periods of diversification above the average background level, e.g. radiations after mass extinction events, without using the equilibrium parameter of the logistic model and its accompanying predictions of diversity-dependent origination and extinction rates, and an upper limit to diversity.
- Tests for competitive interaction and displacement between ecological rather than taxonomic groupings of organisms. This would require ecological data on fossil taxa, and modifications to the TAXONOMIC database to allow such information to be held and manipulated.

6.4. Conclusions of research

- The phylogenetic method of estimating biodiversity is superior to the taxic at capturing the real pattern of diversity when used in analyses of large clades with many extant representatives provided there is no error in phylogenetic reconstruction. Due to the over-estimation of diversity produced by phylogenies with misidentified ancestral taxa, and the skew introduced before mass extinctions and at the end of the diversity history of a clade, the phylogenetic

method is considered inappropriate for studies of extinct groups, particularly those containing few taxa or suffering many significant extinctions.

- The Palaeozoic plateau in marine diversity is evident in empirical curves at ordinal, familial and generic level. Its dominance as a feature of the curves is reduced at lower levels in the taxonomic hierarchy. A species-level model suggests that the plateau is least evident in species curves, with a corresponding increase in the relative importance of the Meso-Cenozoic rise. It is predicted that a species-level Phanerozoic global marine diversity curve will appear exponential.
- Computer simulations suggest that it is unlikely that a large diversity radiation event, followed by an equilibrium, would occur early in the diversification history of a group, if the behaviour of origination and extinction rates was purely stochastic.
- Tests of diversity-dependence of origination and extinction rates through the Palaeozoic demonstrate that origination rate is diversity-dependent through the Ordovician rise, but diversity-independent over the equilibrium period itself. Extinction rate does not display the predicted diversity-dependence at any time, but rather a weak negative trend with increasing diversity.
- From this evidence it is proposed that the Cambro-Ordovician radiations were deterministically driven by origination rate, and characterised by taxa with a high inherent rate of speciation. The Palaeozoic plateau is a stochastic structure, with random rates of origination and extinction, characterised by taxa with a low rate of speciation and high longevity. There is no evidence for an ecological or biologically determined upper limit to diversity.
- Macroevolutionary competitive interactions can be a feature of both exponential and logistic diversification patterns. A competitively maintained equilibrium period, however, is a prediction of the logistic model. Articulate brachiopod diversification fits this model, suggesting an upper limit and subsequent reduction in articulate numbers resulting from competition. Conversely, bivalve diversification follows a pattern of exponential increase. Thus there is no evidence to suggest that bivalve taxa were competing with articulate brachiopod taxa.

LITERATURE CITED

Adrain, J. M., and S. R. Westrop. 2000. An empirical assessment of taxic paleobiology. Science 289:110-112.

Allison, P. A., and D. E. G. Briggs. 1993. Exceptional fossil record: distribution of soft tissue preservation through the Phanerozoic. Geology 21:527-530.

Alroy, J. 1998. Equilibrial diversity dynamics in North American mammals. Pp. 233-287 *in* M. L. McKinney and J. A. Drake, eds. Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia University Press, New York.

---. 1999. The fossil record of North American mammals: Evidence for a Paleocene evolutionary radiation. Systematic Biology 48:107-118.

---. 2000. New methods for quantifying macroevolutionary patterns and processes. Paleobiology 26:707-733.

Alroy, J. (and 25 others). 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. Proceedings of the National Academy of Sciences, U.S.A. 98:6261-6266.

Archibald, J. D. 1994. Metataxon concepts and assessing possible ancestry using Phylogenetic Systematics. Systematic Biology 43:27-40.

Ausich, W. I., and D. J. Bottjer. 1982. Tiering in suspension feeding communities on soft substrata throughout the Phanerozoic. Science 216:173-174.

---. 1985. Phanerozoic tiering in suspension feeding communities on soft substrata: implications for diversity. Pp. 255-274 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.

Bambach, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology 3:152-167.

---. 1985. Classes and adaptive variety: the ecology of diversification in marine faunas through the Phanerozoic. Pp. 191-253 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.

---. 1989. Similarities and differences in diversity patterns at different taxonomic levels using traditional (non-cladistic) groups. Geological Society of America abstracts with program 21:A206-A207.

---. 1999. Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere. Geobios 32:131-144.

Bambach, R. K., and J. B. Bennington. 1996. Do communities evolve? Pp. 123-160 *in* D. Jablonski, D. H. Erwin and J. H. Lipps, eds. Evolutionary paleobiology. Chicago University Press, Chicago.

Barrow, J. D., and F. J. Tipler. The anthropic cosmological principle. Oxford University Press, Oxford, England.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: individuals, populations, and communities. Third edition. Blackwell, Boston.

Benton, M. J. 1985. Mass extinctions among non-marine tetrapods. Nature 316:811-14.

---. 1987. Progress and competition in macroevolution. Biological Reviews 62:305-338.

---. 1989. Mass extinctions among tetrapods and the quality of the fossil record. Philosophical Transactions of the Royal Society B 325:369-86.

---. 1990. Retiles. Pp. 279-300 *in* K. J. McNamara, ed. Evolutionary trends. University Arizona Press, Tucson, AZ.

---, ed. 1993. The fossil record 2. Chapman and Hall, London.

---. 1995. Diversification and extinction in the history of life. Science 268:52-58.

---. 1996. On the nonprevalence of competitive replacement in the evolution of tetrapods. Pp. 185-210 *in* D. Jablonski, D. H. Erwin and J. H. Lipps, eds. Evolutionary paleobiology. Chicago University Press, Chicago.

---. 1997. Models for the diversification of life. Trends in Ecology and Evolution 12:490-495.

---. 1999. The history of life: large databases in palaeontology. Pp. 249-283 *in* D. T. Harper, ed. Numerical Palaeobiology. John Wiley and Sons, Chichester, England.

---. 2000. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? Biological Reviews 75:633-648.

---. 2001. Biodiversity on land and in the sea. Geological Journal 36:211-230.

Benton, M. J., and R. Hitchin. 1996. Testing the quality of the fossil record by groups and by major habitats. Systematic Biology 12:111-157.

Benton, M. J., R. Hitchin, and M. Wills. 1999. Assessing congruence between cladistic and stratigraphic data. Systematic Biology 48:581-596.

Benton, M. J., M. Wills, and R. Hitchin. 2000. Quality of the fossil record through time. Nature 403:534-537.

Bookstein, F. L. 1987. Random walk and the existence of evolutionary rates. Paleobiology 13:446-464.

Bottjer, D. J., and D. Jablonski. 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. Palaios 3:540-560.

Boucot, A. J. 1983. Does evolution take place in a vacuum? Journal of Paleontology 57:1-30.

---. 1990. Phanerozoic extinctions: how similar are they to each other? Pp. 5-30 *in* E. G. Kauffman and O. H. Walliser, eds. Extinction events in Earth history. Springer-Verlag, Berlin.

Bowring, S. A., J. P. Grotzinger, C. E. Isachsen, A. H. Knoll, S. M. Pelechaty, and P. Kolosov. 1993. Calibrating rates of Early Cambrian evolution. Science 261:1293-1298.

Brasier, M. D., and S. S. Sukhov. 1998. The falling amplitude of carbon isotopic oscillations through the Lower to Middle Cambrian: northern Siberia date. Canadian Journal of Earth Sciences 35:353-373.

Brett, C. E., and G. C. Baird. 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. Pp. 285-315 *in* D. H. Erwin and R. L. Anstey, eds. New approaches to speciation in the fossil record. Columbia University Press, New York.

Briggs, J. C. 1994. Species diversity: land and sea compared. Systematic Biology 43:130-135.

Cantino, P. D., H. N. Bryant, K. de Querioz, M. J. Donoghue, T. Eriksson, D. M. Hillis, and M. S. Y. Lee. 1999. Species names in phylogenetic nomenclature. Systematic Biology 48:790-807.

Carr, T. R., and J. A. Kitchell. 1980. Dynamics of taxonomic diversity. Paleobiology 6:427-443.

Carroll, S. B. 2001. Chance and necessity: the evolution of morphological complexity and diversity. Nature 409:1102-1109.

Carter, B. 1974. Large number coincidences and the anthropic principle in cosmology. Pp. 291-298 *in* M. S. Longair, ed. Confrontation of cosmological theories with observational data. Reidel, Dordrecht, Netherlands.

Connor, E. F. 1986. Time series analysis in the fossil record. Pp. 119-147 *in* D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Springer-Verlag, Berlin.

Conway Morris, S. 1998. The evolution of diversity in ancient ecosystems: a review. Philosophical Transactions of the Royal Society of London B 353:327-345.

Courtillot, V., and Y. Gaudemer. 1996. Effects of mass extinctions on biodiversity. Nature 381:146-148.

Cowen, R., and W. L. Stockton. 1978. Testing for evolutionary equilibria. Paleobiology 4:195-200.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London.

Davidek, K., E. Landing, S. A. Bowring, S. R. Westrop, A. W. A. Rushton, R. A. Fortey, and J. M. Adrain. 1998. New uppermost Cambrian U-Pb date from Avalonian Wales and age of the Cambrian-Ordovician boundary. Geological Magazine 135:305-309.

Doyle, J. A., and M. J. Donoghue. 1993. Phylogenies and angiosperm diversification. Paleobiology 19:141-167.

Eldredge, N. 1996. Hierarchies and macroevolution. Pp. 42-61 *in* D. Jablonski, D. H. Erwin and J. H. Lipps, eds. Evolutionary paleobiology. Chicago University Press, Chicago.

Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: An alternative to phyletic gradualism. Pp. 82-115 *in* T. J. M. Schopf, ed. Models in paleobiology. Freeman Cooper, San Francisco.

Emilliani, C. 1982. Extinctive evolution – Extinctive and competitive evolution combine into a unified model of evolution. Journal of theoretical biology 97:13-33.

Enquist, B. J., J. P. Haskell, and B. H. Tiffney. 2002. General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. Nature 419:610-613.

Erwin, D. H., and S. L. Wing, eds. 2000. Deep time: *Paleobiology's* perspective. Paleobiology 26(Suppl. to No. 4):53-73.

Fara, E. 2001. What are lazarus taxa? Geological Journal 36:291-303.

Flessa, K. W., and J. Imbrie. 1973. Evolutionary pulsations: Evidence from Phanerozoic diversity patterns. Pp. 247-285 *in* D. H. Tarling and S. K. Runcorn, eds. Implications of continental drift to the earth sciences. Academic Press, London.

Flessa, K. W., and J. S. Levinton. 1975. Phanerozoic diversity patterns: tests for randomness. Journal of Geology 83:239-248.

Flessa, K. W., and D. Jablonski. 1985. Declining Phanerozoic background extinction rates: effect of taxonomic structure? Nature 313:216-218.

Foote, M. 1994. Temporal variation in extinction risk and temporal scaling of extinction metrics. Paleobiology 20:424-444.

---. 1996a. Perspective: evolutionary patterns in the fossil record. Evolution 50:1-11.

---. 1996b. On the probability of ancestors in the fossil record. Paleobiology 22:141-151.

---. 2000a. Origination and extinction components of taxonomic diversity: general problems. *In* D. H. Erwin and S. L. Wing, eds. Deep time: *Paleobiology's* perspective. Paleobiology 26(Suppl. to No. 4):74-102.

---. 2000b. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. Paleobiology 26:578-605.

---. 2001. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. Paleobiology 27:602-630.

Foote, M., and D. M. Raup. 1996. Fossil preservation and the stratigraphic ranges of taxa. Paleobiology 22:121-140.

Foote, M., and J. J. Sepkoski Jr. 1999. Absolute measures of the completeness of the fossil record. Nature 398:415-417.

Gause, G. F. 1934. Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. Science 79:16-17.

Gilinsky, N. L. 1994. Volatility and the Phanerozoic decline of background extinction intensity. Paleobiology 20:445-468.

Gilinsky, N. L., and R. K. Bambach. 1987. Asymmetrical patterns of origination and extinction in higher taxa. Paleobiology 13: 427-445.

Godfray, H. C. J. 2002. Challenges for taxonomy. Nature 417:17-19.

Gould, S. J. 1983. Mind and supermind. Natural history 92:34-38.

Gould, S. J., D. M. Raup, J. J. Sepkoski, Jr., T. J. M. Schopf, and D. S. Simberloff. 1977. The shape of evolution: A comparison of real and random clades. Paleobiology 3:23-40.

Gould, S. J., and C. B. Calloway. 1980. Clams and Brachiopods – ships that pass in the night. Paleobiology 6:383-396.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane, and J.

McNeill. 1994. International Code of Botanical Nomenclature (Tokyo Code).

Regnum Vegetabile 131. Koeltz Scientific Books, Königstein.

Harland, W. B., R. L. Armstrong, A. V. Cox, L. E. Craig, A. G. Smith, and D. G. Smith. 1990. A geologic time scale. Cambridge University Press, Cambridge, England.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, England.

Hennig, W. 1965. Phylogenetic systematics. University of Illinois Press, Urbana, Ill.

Hoffman, A. 1985. Patterns of family extinction: dependence on definition and geologic time scale. Nature 315:659-662.

---. 1986. Neutral model of Phanerozoic diversification: implications for macroevolution. Neues Jahrbuch fur Geologische und Palaontologis che Abhandleungen 172:219-244.

---. 1989. Arguments on evolution: a paleontologist's perspective. Oxford University Press, Oxford, England.

Hoffman, A., and J. Ghiold. 1985. Randomness in the pattern of 'mass extinctions' and 'waves of origination'. Geological Magazine 122:1-96.

Hoffman, A., and E. J. Fenster. 1986. Randomness and diversification in the Phanerozoic: A simulation. Palaeontology 29:655-663.

Huelsenbeck, J. P. 1991. When are fossils better than extant taxa in phylogenetic analysis? Systematic Zoology 40:458-469.

International Trust for Zoological Nomenclature. 1999. International code of zoological nomenclature, 4th edition. London.

Jablonski, D., and D. M. Raup. 1995. Selectivity of the end-Cretaceous marine bivalve extinctions. Science 268:389-391.

Jeffery, C. H. 2001. Heart urchins at the Cretaceous/Tertiary boundary: a tale of two clades. Paleobiology 27:140-158.

Johnson, K. G., and T. McCormick. 1999. The quantitative description of biotic changes using palaeontological databases. Pp. 226-247 *in* D. T. Harper, ed. Numerical Palaeobiology. John Wiley and Sons, Chichester, England.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636-638.

Kemp, T. S. 1999. Fossils and evolution. Oxford University Press, Oxford, England.

Kirchner, J. W., and A. Weil. 2000a. Delayed biological recovery from extinctions throughout the fossil record. Nature 404:177-180.

---. 2000b. Correlations in fossil extinction and origination rates through geological time. Proceedings of the Royal Society of London B 267:1301-1309.

Kitchell, J. A., and T. R. Carr. 1985. Nonequilibrium model of diversification: faunal turnover dynamics. Pp. 277-309 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.

Knapp S., R. M. Bateman, N. R. Chalmers, C. J. Humphries, P. S. Rainbow, A. B. Smith, P. D. Taylor, R. I. Vane-Wright, and M. Wilkinson. 2002. Taxonomy needs evolution, not revolution. Nature 419:559.

Kuno, E. 1991. Some strange properties of the logistic equation defined with *r* and *K*: inherent defects or artifacts? Researches on Population Ecology 33:33-39.

Landing, E. 1994. Precambrian-Cambrian boundary ratified and new perspective of Cambrian time. Geology 22:179-182.

Landing, E., S. A. Bowring, K. L. Davidek, S. R. Westrop, G. Geyer, and W. Heldmaier. 1998. Duration of the Early Cambrian: U-Pb ages of volcanic ashes from Avalon and Gondwana. Canadian Journal of Earth Sciences 35:329-338.

Levinton, J. 1988. Genetics, paleontology, and macroevolution. Cambridge University Press, Cambridge, England.

Lidgard, S., F. K. McKinney, and P. D. Taylor. 1993. Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity. Paleobiology 19:352-371.

Maas, M. C., D. W. Krause, and S. G. Strait. 1988. The decline and extinction of Pleisiadapiformes (Mammalia: ?Primates) in North America: displacement or replacement? Paleobiology 14:410-431.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Marshall, C. R. 1990. Confidence intervals on stratigraphic ranges. Paleobiology 16:1-10.

---. 1991. Estimation of taxonomic ranges from the fossil record. Pp. 19-38 *in* N. L. Gilinsky and P. W. Signor, eds. Analytical paleobiology. Short courses in paleontology 4. The Paleontological Society, Knoxville, Tenn.

Maxwell, W. D., and M. J. Benton. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. Paleobiology 16:322-335.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge.

---. 1974. Cladistic analysis or cladistic classification. Zeit schrift für Zoologische Systematik und Evolutionforschung 12:94-128.

McCormick, T., and A. W. Owen. 2001. Assessing trilobite biodiversity change in the Ordovician of the British Isles. Geological Journal 36:279-290.

McGowan, A. J., and P. N. Pearson. 1999. ADAPTS (Analysis of Diversity, Asymmetry of Phylogenetic Trees, and Survivorship): a new software tool for analysing stratigraphic range data. Palaeontologica Electronica 2: Issue 1.

McKinney, M. L., and J. A. Drake, eds. 1998. Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia University Press, New York.

Miller, A. I. 1988. Spatio-temporal transitions in Paleozoic Bivalvia: An analysis of North American fossil assemblages. Historical Biology 1:251-273.

---. 2000. Conversations about Phanerozoic global diversity. *In* D. H. Erwin and S. L. Wing, eds. Deep time: *Paleobiology's* perspective. Paleobiology 26(Suppl. to No. 4):53-73.

Miller, A. I., and J. J. Sepkoski Jr. 1988. Modeling bivalve diversification. The effect of interaction on a macroevolutionary system. Paleobiology 14:364-369.

Miller, A. I., and M. Foote. 1996. Calibrating the Ordovician radiation of life: Implications for Phanerozoic diversity trends. Paleobiology 22:304-309.

Moore, R. C., Teichert, C., Robison, R. A., and Kaesler, R. L. 1953-2000. Treatise on Invertebrate Paleontology. Geological Society of America and University of Kansas Press, Lawrence, KS.

Newman, M. E. J., and P. Sibani. 1999. Extinction, diversity and survivorship of taxa in the fossil record. Philosophical Transactions of the Royal Society of London B 266:1593-1599.

Newman, M. E. J., and G. J. Eble. 1999. Decline in extinction rates and scale invariance in the fossil record. Paleobiology 25:434-439.

Niklas, K. J. 1986. Large-scale changes in animal and plant terrestrial communities. Pp. 383-405 *in* D. M. Raup, and D. Jablonski eds. Patterns and processes in the history of life. Springer-Verlag, Berlin.

Niklas, K. J., B. H. Tiffney, and A. H. Knoll. 1985. Patterns in vascular land plant diversification: an analysis at the species level. Pp. 97-128 *in* J. W. Valentine ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, NJ.

Norell, M. A. 1992. Taxic origin and temporal diversity: The effect of phylogeny. Pp. 89-118 *in* M. J. Novacek and Q. D. Wheeler, eds. Extinction and phylogeny. Columbus University Press, New York.

---. 1993. Tree-based approaches to understanding history: Comments on ranks, rules, and the quality of the fossil record. American Journal of Science 293-A:407-417.

Norell, M. A., and M. J. Novacek. 1992a. Congruence between superpositional and phylogenetic patterns: Comparing cladistic patterns with fossil evidence. Cladistics 8:319-337.

---. 1992b. The fossil record and evolution: Comparing cladistic and paleontologic evidence for vertebrate history. Science 255:1690-1693.

Novacek, M. J., and M. A. Norell. 1982. Fossils, phylogeny, and taxonomic rates of evolution. Systematic Zoology 31:266-275.

Omland, K. E. 1997. Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabble ducks (Anatini). Evolution 51:1636-1646.

Palmer, A. R. 1998. A proposed nomenclature for stages and series for the Cambrian of Laurentia. Canadian Journal of Earth Sciences 35:323-328.

Patterson, C., and A. B. Smith. 1987. Is the periodicity of extinction a taxonomic artefact? Nature 330:248-251.

---. 1989. Periodicity in extinction: the role of systematics. Ecology 70:802-811.

Patzkowsky, M. E., and S. M. Holland. 1997. Patterns of turnover in Middle and Upper Ordovician brachiopods of the eastern United States: a test of coordinated stasis. Paleobiology 23: 420-443.

Paul, C. R. 1979. Early echinoderm radiation. Systematics Association Special Publication 12: 415-434.

---. 1990. Completeness of the fossil record. Pp. 298-303 *in* D. E. G. Briggs and P. R. Crowther, eds. Palaeobiology: a synthesis. Blackwell Science, Oxford, England.

Pearson, P. N. 1998. Speciation and extinction asymmetries in palaeontological phylogenies: evidence for evolutionary progress? Paleobiology 24:305-335.

Pearson, P. N., N. J. Shackleton, and M. A. Hall. 1997. Stable isotope evidence for the sympatric divergence of *Globigerinoides trilobus* and *Orbulina universa* (planktonic foraminifera). Journal of the Geological Society of London 154:295-302.

Peters, S. E., and M. Foote. 2001. Biodiversity in the Phanerozoic: a reinterpretation. Paleobiology 27:583-601.

---. 2002. Determinants of extinction in the fossil record. Nature 416:420-424.

Przeworski, M., and J. D. Wall. 1998. An evaluation of a hierarchical branching process as a model for species diversification. Paleobiology 24:498-511.

Purvis, A., P. Agapow, J. L. Gittleman, and G. M. Mace. Nonrandom extinction and the loss of evolutionary history. Science 288:328-330.

Raup, D. M. 1972. Taxonomic diversity during the Phanerozoic. Science 231:1065-1071.

---. 1975. Taxonomic diversity estimation using rarefaction. Paleobiology 1:333-342.

---. 1977. Stochastic models in evolutionary palaeontology. Pp. 59-78 *in* A. Hallam, ed. Patterns of evolution as illustrated by the fossil record. Elsevier, Amsterdam, Neatherlands.

---. 1979a. Biases in the fossil record of species and genera. Bulletin of the Carnegie Museum of Natural History 13:85-91.

---. 1979b. Size of the Permo-Triassic bottleneck and its evolutionary implications. Science 206:217-218.

---. 1983. On the early origins of major biologic groups. Paleobiology 9:107-115.

---. 1985. Mathematical modeling of cladogenesis. Paleobiology 11:42-52.

---. 1995. The role of extinction in evolution. Pp. 109-124 *in* W. M. Fitch and F. J. Ayala, eds. Tempo and mode in evolution: genetics and paleontology 50 years after Simpson. National Academy Press, Washington DC.

Raup, D. M., S. J. Gould, J. M. Schopf, and D. S. Simerloff. 1973. Stochastic models of phylogeny and the evolution of diversity. Journal of Geology 81:525-541.

Raup, D. M., and D. Jablonski, eds. 1986. Patterns and processes in the history of life. Springer-Verlag, Berlin.

Raup, D. M., and J. J. Sepkoski Jr. 1982. Mass extinctions in the marine fossil record. Science 215:1501-1503.

---. 1984. Periodicity of extinction in the geologic past. Proceedings of the National Academy of Sciences USA 81:801-505.

Robeck H. E., C. C. Maley, and M. J. Donoghue. 2000. Taxonomy and temporal diversity patterns. Paleobiology 26:171-187.

Rosenzweig, M. L. 1975. On continental steady states of species diversity. Pp. 121-140 *in* M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknapp Press, Cambridge, Mass.

Rosenzweig, M. L., and R. D. McCord. 1991. Incumbent replacement: evidence for long-term evolutionary progress. Paleobiology 17:202-213.

Roy, K., D. Jablonski, and J. W. Valentine. 1996. Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs. Philosophical Transactions of the Royal Society of London, B 351:1605-1613.

Sepkoski, J. J., Jr. 1978. A kinetic model of Phanerozoic taxonomic diversity: I. Analysis of marine orders. Paleobiology 4:223-251.

---. 1979. A kinetic model of Phanerozoic taxonomic diversity: II. Early Phanerozoic families and multiple equilibria. Paleobiology 5:222-251.

---. 1981. A factor analytic description of the Phanerozoic marine fossil record. Paleobiology 7:36-53.

---. 1984. A kinetic model of Phanerozoic taxonomic diversity: III. Post-Paleozoic families and mass extinctions. Paleobiology 10:246-267.

---. 1992. A compendium of fossil marine animal families, 2nd edition. Milwaukee Public Museum Contributions in Biology and Geology 83:1-156.

---. 1993. Ten years in the library: new data confirm paleontological patterns. Paleobiology 19:43-51.

---. 1996a. Competition in macroevolution. Pp. 211-255 *in* D. Jablonski, D. H. Erwin and J. H. Lipps, eds. Evolutionary paleobiology. Chicago University Press, Chicago.

---. 1996b. Patterns of Phanerozoic extinctions: a perspective from global databases. Pp. 35-52 *in* O. H. Walliser, ed. Global events and event stratigraphy. Springer-Verlag, Berlin.

---. 1997. Biodiversity: past, present, and future. Journal of Paleontology 7:533-539.

---. 1998a. Analysing diversification through time. Trends in Ecology and Evolution 13:158-159.

---. 1998b. Rates of speciation in the fossil record. Philosophical Transactions of the Royal Society of London B 353:315-326.

Sepkoski, J. J., Jr., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. Nature 293: 435-437.

Sepkoski, J. J., Jr., and A. I. Miller. 1985. Evolutionary faunas and the distribution of Paleozoic benthic communities in time and space. Pp. 153-190 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: models in macroevolution. Princeton University Press, Princeton, N.J.

Sepkoski, J. J., Jr., and D. C. Kendrick. 1993. Numerical experiments with model monophyletic and paraphyletic taxa. Paleobiology 19:168-184.

Shaw, A. B. 1964. Time in stratigraphy. McGraw-Hill, New York.

Sheehan, P. M. A new look at Ecologic Evolutionary Units (EEUs): Palaeogeography, Palaeoclimatology, Palaeoecology 127:21-32.

Shergold, J. H. 1995. Timescales 1. Cambrian. Australian Geological Survey Organisation, Record 1995/30.

Signor, P. W. 1985. Real and apparent trends in species richness through time. Pp. 129-150 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.

---. 1990. The geologic history of diversity. Annual Review of Ecology and Systematics 21:509-539.

---. 1995. The role of extinction in evolution. Pp. 109-124 *in* W. M. Fitch and F. J. Ayala, eds. Tempo and mode in evolution: genetics and paleontology 50 years after Simpson. National Academy Press, Washington, D.C.

Signor, P. W., and J. H. Lipps. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. Geological Society of America Special Paper 190:291-296.

Simpson, G. G. 1961. Principles of animal taxonomy. Columbia University Press, New York.

Skelton, P. W., E. Gili, B. R. Rosen, and F.X. Valldeperas. 1997. Corals and rudists in the late Cretaceous: a critique of the hypothesis of competitive displacement. Boletín de la Real Sociedad Española de Historia Natural (seccíon geológica) 92:225-239.

Smith, A. B. 1988. Patterns of diversification and extinction in early Palaeozoic echinoderms. Palaeontology 31:799-828.

---. 1994. Systematics and the fossil record. Blackwell Science, Oxford, England.

Smith, A. B., and C. Patterson. 1988. The influence of taxonomy on the perception of patterns of evolution. Evolutionary Biology 23:127-216.

Smith, A. B., A. S. Gale, and N. E. A. Monks. Sea-level change and rock-record bias in the Cretaceous: a problem for extinction and biodiversity studies. Paleobiology 27:241-253.

Sneath, P. H. A. Ed. 1992. International Code of Nomenclature of Bacteria, 1980 Revision. Washington.

Solow, A., and W. Smith. 1997. On fossil preservation and the stratigraphic ranges of taxa. Paleobiology 23:271-277.

Stanley, S. M., P. W. Signor III, S. Ligard, and A. F. Karr. 1981. Natural clades differ from "random" clades: simulations and analyses. Paleobiology 7:115-127.

Strauss, D., and P. M. Sadler. 1989. Confidence intervals and Bayesian probability estimates for ends of local taxon ranges. Mathematical Geology 21:411-427.

Thayer, C. W. 1983. Sediment-mediated biological disturbance and the evolution of the marine benthos. Pp. 474-669 *in* M. J. S. Tevesz and P. M. McCall, eds. Biotic interactions in recent and fossil benthic communities. Plenum, New York.

Thompson, J. N., and B. M. Cunningham. 2002. Geographic structure and dynamics of coevolutionary selection. Nature 417:735-738.

Valentine, J. W. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic times. Palaeontology 12:684-709.

---, ed. 1985. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.

---. 1990. The macroevolution of clade shape. Pp. 128-150 *in* R. M. Ross and W. D. Allmon, eds. Causes of evolution: A palaeontological perspective. University of Chicago Press, Chicago.

Van Valen, L. M. 1973. A new evolutionary law. Evolutionary Theory 1:11-30.

---. 1984. A resetting of Phanerozoic community evolution. Nature 307:50-52.

Vermeij, G. J. 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. Paleobiology 3:245-258.

---. 1995. Economics, volcanoes, and Phanerozoic revolutions. Paleobiology 21:125-152.

---. 1987. Evolution and escalation: an ecological history of life. Princeton University Press, Princeton, N.J.

Vrba, E. S. 1993. Turnover-pulses, the Red Queen, and related topics. American Journal of Science 293-A:418-452.

Wagner, P. J. 1995. Diversity patterns among early gastropods: contrasting taxonomic and phylogenetic descriptions. Paleobiology 21:410-439.

---. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. Systematic Biology 49:65-86.

Wagner, P. J., and D. H. Erwin. 1995. Phylogenetic tests of speciation hypotheses. Pp. 87-122 *in* D. H. Erwin, and R. L. Anstey, eds. New approaches to studying speciation in the fossil record. Columbia University Press, New York.

Walker, T. D. 1985. Diversification functions and the rate of taxonomic evolution. Pp. 311-334 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.

Walker, T. D., and J. W. Valentine. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. American Naturalist 124:887-899.

Ward, P. D., and P. W. Signor. 1985. Pp. 399-418 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.

Wei, Kuo-Yen, and J. P. Kennett. 1986. Taxonomic evolution of Neogene planktonic foraminifera and paleoceanographic relations. Paleoceanography 1:67-84.

Westrop, S. R., and J. A. Adrain. 1998. Trilobite alpha diversity and the reorganization of Ordovician benthic marine communities. Paleobiology 24:1-16.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213-251.

---. 1977. Evolution of species diversity in land communities. Evolutionary Biology 10:1-67.

APPENDIX I: SOURCE CODE

Appendix Ia. GHOSTRANGE program

Source code for the GHOSTRANGE program is provided here. The full listing for the GHOSTRANGE_A version of the program is given below. Lines of code shown in **bold** are those that are substituted for the alternative code in the GHOSTRANGE_B version of the program (see Chapter 2, Section 2.2.2.). This alternative code is shown in **bold** at the end of the program listing.

Both versions of the program are included on the IBM disc accompanying this thesis. The code is written in the C programming language, source code comments are included and are indicated by /* */.

Source code listing for GHOSTRANGE_A:

```
/*A PROGRAM TO ANALYSE THE ADDITION OF GHOST RANGES*/
/*TO DIVERSITY COUNTS*/

/*HEADER FILES*/
#include<stdio.h>
#include<conio.h>
#include<stdlib.h>
#include<string.h>
#include<time.h>
#include<math.h>

/*STRUCTURE DEFINITIONS*/

/*definition of taxon type dynamic data structure*/
typedef struct tax_t
{
        /*id number*/
        int id;
        /*generation*/
        int gen;
        /*Actual first and last appearance*/
        int af,al;
        /*Sampled first and last appearance*/
        int sf,sl;
        /*phylogenetic first and last appearance*/
        int pf,pl;
        /*self referential pointer to ancestor and sister*/
        struct tax_t *anc, *sis;
        /*self referential pointers to two descendents*/
        struct tax_t *d1, *d2;
}taxon_t;

/*definition of time step structure to hold results*/
struct timestep_t
{
        /*real, uncorrected and corrected diversity*/
        int rd,ud,cd;
        /*time detrended real, uncorrected and corrected diversity*/
        float rd_dtr, ud_dtr, cd_dtr;
        /*uncorrected and corrected diversity magnitude (% of real diversity)*/
```

```
        int ud_mag, cd_mag;
};

/*FUNCTION PROTOTYPES*/

/*function to create a taxon node*/
taxon_t *create_taxon(taxon_t *anc, int first, int last, int gen);
/*function to grow tree*/
void grow_tree(taxon_t *current, int step, int chop, float o_rate, float e_rate, int
eqdiv);

/*function to print tree*/
void print_tree(taxon_t *current, int corr);

/*function to sample phylogeny*/
void sample_taxa(taxon_t *current,int step,int chop,char pull,char anc_on,float
s_rate);

/*function to count diversity*/
void count_taxa(taxon_t *current, int step, int *count1, int *count2, int corr, char
sin);

/*function to free all memory used by tree*/
void free_memory(taxon_t *current, int snap);

/*function to add ghost ranges to phylogeny*/
void set_ghost_range(taxon_t *current);

/*functions to return nearest sampled relative*/
taxon_t *find_relative(taxon_t *current);
taxon_t *search(taxon_t *current, int gen);

/*function to get diversity dependent origination rate*/
float get_origination_rate(float o_rate, float e_rate, int eqdiv);

/*function to create duplicate phylogeny*/
void copy_tree(taxon_t *copy, taxon_t *master);

/*function to get r2, the product-moment correlation coefficient*/
float get_correlation_coefficient(int n,float sum_xy,float sum_x,float sum_y,float
sum_x2,float sum_y2);

/*RANROT random number generator*/

/* define desired integer type */
typedef  unsigned int my_uint;

/* If your system doesn't have a rotate function for the chosen integer type
   then define it thus:                                                    */
my_uint rotl (my_uint x, my_uint r) {
  return (x << r) | (x >> (sizeof(x)*8-r));}

/* define parameters (R1 and R2 must be smaller than the integer size): */
#define KK  17
#define JJ  10
#define R1   5
#define R2   3

/* global variables */
my_uint randbuffer[KK];  /* history buffer */
int r_p1, r_p2;          /* indexes into history buffer */
float scale;             /* 2^(- integer size) */

void RanrotAInit (my_uint seed);
double RanrotA();

/*GLOBAL VARIABLES*/

/*id_v, *id == variable and pointer for keeping track of id number*/
int id_v = 1, *id = &id_v;
/*variable and pointer to keep track of standing diversity*/
int stdiv_v = 1, *stdiv = &stdiv_v;
/*variable to set last generation*/
int last_gen;
/*structure to hold master root, root and last taxa*/
taxon_t *m_root=NULL, *root=NULL, *last=NULL;
/*mass extinction rate*/
```

```
float mass_rate = 0.9;

/*MAIN*/

main()
{

        /*variables and pointers for keeping track of diversity counts*/
        int count1_v, *count1 = &count1_v;
        int count2_v, *count2 = &count2_v;

        /*chop == maximum number of time steps possible*/
        /*s == time step of tree*/
        /*lin == number of lineages, eqdiv == equilibrium diversity*/
        int     chop = 1000, s, lin, eqdiv, x=0;
        /*options to have ancestors,'pull of the recent', mass extinctions & singletons
included*/
        char anc_on, pull, mass, sin, next_run;
        /*variables to hold origination rate, extinction rate and sampling rate as
input by user*/
        /*mass extinction rate set*/
        float o_rate,e_rate,s_rate;

        /*variables to hold regression line and correlation coefficient calculations*/
        float sum_rd, sum_ud, sum_cd, sum_rd2, sum_ud2, sum_cd2, sum_rdud, sum_rdcd;
        float r2_ud, r2_cd, par_r2_ud, par_r2_cd;
        float sum_time2, sum_timerd, sum_timeud, sum_timecd;
        float rd_pred, ud_pred, cd_pred;
        float b_rd, b_ud, b_cd;

        /*variables to hold maximum and minimum diversity magnitude metrics*/
        int mag_max_ud, mag_min_ud, mag_max_cd, mag_min_cd;

        /*file name strings*/
        char file_name1[31],mfile_name[34],file_name2[34];

        /*array of step structures to hold data for each time_step*/
        struct timestep_t step[1000]={{0}};

        /*file pointers*/
        FILE *fp,*mfp;


        /*print title*/
        printf("GHOSTRANGE_A: To analyse the addition of ghost ranges to diversity
counts.\n\n");
        /*get user input*/
        printf("Enter parameters for phylogeny generation");
        printf("\n\nEnter number of lineages to create: ");
        scanf(" %i", &lin);
        printf("\nEnter initial origination rate 0-1: ");
        scanf(" %f", &o_rate);
        printf("\nEnter initial extinction rate 0-1: ");
        scanf(" %f", &e_rate);
        printf("\nEnter equilibrium diversity (0 for exponential growth): ");
        scanf(" %i", &eqdiv);
        printf("\nDo you want mass extinctions included? y/n: ");
        scanf(" %c", &mass);
        printf("\nEnter phylogeny file name (Max 30 characters, no spaces): ");
        scanf(" %s", file_name1);

        printf("\nPress any key to generate phylogeny");
        getch();

        fflush(stdin);

        /*create 1st and last taxon, with NULL ancestor, id of 1, first appearance of
1, generation no of 1*/
        m_root = last = create_taxon(NULL,1,chop,1);

        /* initialize, using time as random seed */
        RanrotAInit(time(0));

        /*GROW TREE*/
        /*run through time sequence from 2nd time step*/
        for(s=2;s<chop;s++)
        {
```

```
                /*if mass extinctions are on, every 20 time steps, increase the
extinction rate*/
                if(mass=='y' && s%20==0)
                {
                        /*traverse tree to grow new branches*/
                        grow_tree(m_root,s,chop,o_rate,mass_rate,eqdiv);
                }
                else
                {
                        /*traverse tree to grow new branches*/
                        grow_tree(m_root,s,chop,o_rate,e_rate,eqdiv);

                }
                        /*if the correct number of taxa have been produced, end tree growth*/
                        if(*id >= lin)
                        {
                                s++;
                                break;
                        }
        }

        /*if the tree has grown for 1000 steps without producing desired number of
taxa*/
        if(s==chop)
        {
                printf("\n\n%i lineages were not produced within 1000 time steps",lin);
                printf("\n\n0Press key to end program\n\n");
                getch();
                /*end program*/
                exit(1);
        }

        /*set the final time step to equal the time step reached*/
        chop = s;
        /*set number of lineages to equal id*/
        lin = *id;

        /*open master file*/
        sprintf(mfile_name, "%s.xls", file_name1);
        if((mfp = fopen(mfile_name,"w"))==NULL)
        {
                printf("\n\nCannot open file \n");
                exit(1);
        }
        fprintf(mfp,"File\tLineages\tTime
steps\tko\tke\tDeq\tMEx\tSI\tPR\tAnc\tS_tons\tUncorrected Diversity
Statistics\t\t\tCorrected Diversity Statistics\n");
        fprintf(mfp,"\t\t\t\t\t\t\t\t\t\tmag(max)\tmag(min)\tr2\tp_r2\tmag(max)\tmag(
min)\tr2\tp_r2\n");

        printf("\n\nPhylogeny created. %i lineages produced in %i time steps", lin,s);
        printf("\n\nPress any key to run analysis");
        getch();

        /*ANALYSIS LOOP*/
        do
        {

                /*set max and min diversity magnitude variables to zero*/
                mag_max_ud = mag_max_cd = 0;
                mag_min_ud = mag_min_cd = 100;

                printf("\n\nEnter sampling rate 0-1: ");
                scanf(" %f", &s_rate);
                printf("\nDo you want to simulate 'pull of the recent'? y/n: ");
                scanf(" %c", &pull);
                printf("\nDo you want ancestor taxa to be included when adding ghost
ranges? y/n: ");
                scanf(" %c", &anc_on);
                printf("\nDo you want singleton taxa included in diversity counts? y/n:
");
                scanf(" %c", &sin);

                fflush(stdin);
```

```
/*CREATE DUPLICATE TREE*/
root = create_taxon(NULL,0,0,0);
copy_tree(root,m_root);


/*SAMPLE TREE*/
/*run through time sequence*/
for(s=1;s<=chop;s++)
{
        /*traverse tree to sample taxa*/
        sample_taxa(root,s,chop,pull,anc_on,s_rate);
}

/*CALCULATE DIVERSITY - REAL AND UNCORRECTED DATA*/

/*run through time sequence*/
for(s=1;s<=chop;s++)
{
        *count1 = *count2 = 0;
        /*traverse tree to count number of taxa - real and uncorrected
(i.e. corr==0)*/
        count_taxa(root, s, count1, count2, 0, sin);
        /*write result of count to appropriate data member*/
        step[s].rd = *count1;
        step[s].ud = *count2;

        /*if neither count is zero, calculate diversity magnitude and
write to data member*/
        if(step[s].ud!=0 && step[s].rd!=0)
        {
                step[s].ud_mag = (step[s].ud*100)/step[s].rd;
        }
        /*else reset magnitude data member to 0*/
        else
        {
                step[s].ud_mag = 0;
        }

        /*if diversity magnitude is greater than previous maximum, set
as new maximum*/
        if(step[s].ud_mag > mag_max_ud)
        {
                mag_max_ud = step[s].ud_mag;
        }

        /*if diversity magnitude is less than previous minimum, set as
new minimum*/
        if(step[s].ud_mag < mag_min_ud && step[s].ud_mag != 0)
        {
                mag_min_ud = step[s].ud_mag;
        }

}


/*ADD GHOST RANGES*/
set_ghost_range(last);


/*CALCULATE DIVERSITY - CORRECTED DATA*/

/*run through time sequence*/
for(s=1;s<=chop;s++)
{
        *count2 = 0;
        /*traverse tree to count number of taxa - corrected (i.e.
corr==1)*/
        count_taxa(root,s,count1,count2,1,sin);
        step[s].cd = *count2;

        /*calculate diversity magnitude*/
        if(step[s].cd!=0 && step[s].rd!=0)
        {
                step[s].cd_mag = (step[s].cd*100)/step[s].rd;
        }
        /*else reset magnitude data member to 0*/
        else
```

```
                {
                        step[s].cd_mag = 0;
                }

                /*if diversity magnitude is greater than previous maximum, set
as new maximum*/
                if(step[s].cd_mag > mag_max_cd)
                {
                        mag_max_cd = step[s].cd_mag;
                }

                /*if diversity magnitude is less than previous minimum, set as
new minimum*/
                if(step[s].cd_mag < mag_min_cd && step[s].cd_mag != 0)
                {
                        mag_min_cd = step[s].cd_mag;
                }
        }

        /*CALCULATE CORRELATION METRICS*/

        /*set all sum variables to zero*/
        sum_time2 = sum_timerd = sum_timeud = sum_timecd = 0;
        sum_rd = sum_ud = sum_cd = sum_rd2 = sum_ud2 = sum_cd2 = sum_rdud =
sum_rdcd = 0;

        for(s=1;s<=chop;s++)
        {

                /*increment sums required for regression line calculations*/
                sum_time2 = sum_time2+(s*s);
                sum_timerd = sum_timerd+(s*step[s].rd);
                sum_timeud = sum_timeud+(s*step[s].ud);
                sum_timecd = sum_timecd+(s*step[s].cd);

                /*increment diversity data sums required for product-moment
correlation*/
                sum_rd = sum_rd + step[s].rd;
                sum_ud = sum_ud + step[s].ud;
                sum_cd = sum_cd + step[s].cd;
                sum_rd2 = sum_rd2 + (step[s].rd*step[s].rd);
                sum_ud2 = sum_ud2 + (step[s].ud*step[s].ud);
                sum_cd2 = sum_cd2 + (step[s].cd*step[s].cd);
                sum_rdud = sum_rdud + (step[s].rd*step[s].ud);

                sum_rdcd = sum_rdcd + (step[s].rd*step[s].cd);

        }

        /*calculate product-moment correlation coefficient for uncorrected and
corrected data*/
        r2_ud =
get_correlation_coefficient(chop,sum_rdud,sum_rd,sum_ud,sum_rd2,sum_ud2);
        r2_cd =
get_correlation_coefficient(chop,sum_rdcd,sum_rd,sum_cd,sum_rd2,sum_cd2);

        /*re-set all sum variables to zero*/
        sum_rd = sum_ud = sum_cd = sum_rd2 = sum_ud2 = sum_cd2 = sum_rdud =
sum_rdcd = 0;

        /*calculate regression line parameters*/
        b_rd = sum_timerd/sum_time2;
        b_ud = sum_timeud/sum_time2;
        b_cd = sum_timecd/sum_time2;

        /*run through time steps, calculating residuals (time de-trended data)
and sums required
        for partial correlation coefficient*/
        for(s=1;s<=chop;s++)
        {
                /*calculate predicted values of diversity from regression
equations*/
                rd_pred = s*b_rd;
                ud_pred = s*b_ud;
                cd_pred = s*b_cd;

                /*calculate residual diversity, or time detrended data*/
```

```
                        step[s].rd_dtr = step[s].rd - rd_pred;
                        step[s].ud_dtr = step[s].ud - ud_pred;
                        step[s].cd_dtr = step[s].cd - cd_pred;

                        /*increment diversity data sums required for partial product-
moment correlation*/
                        sum_rd = sum_rd + step[s].rd_dtr;
                        sum_ud = sum_ud + step[s].ud_dtr;
                        sum_cd = sum_cd + step[s].cd_dtr;
                        sum_rd2 = sum_rd2 + (step[s].rd_dtr*step[s].rd_dtr);
                        sum_ud2 = sum_ud2 + (step[s].ud_dtr*step[s].ud_dtr);
                        sum_cd2 = sum_cd2 + (step[s].cd_dtr*step[s].cd_dtr);
                        sum_rdud = sum_rdud + (step[s].rd_dtr*step[s].ud_dtr);

                        sum_rdcd = sum_rdcd + (step[s].rd_dtr*step[s].cd_dtr);
                }

                /*calculate partial correlation coefficient for detrended uncorrected
and corrected data*/
                par_r2_ud =
get_correlation_coefficient(chop,sum_rdud,sum_rd,sum_ud,sum_rd2,sum_ud2);
                par_r2_cd =
get_correlation_coefficient(chop,sum_rdcd,sum_rd,sum_cd,sum_rd2,sum_cd2);


                /*WRITE DATA TO FILES*/

                /*construct file name*/
                x++;
                sprintf(file_name2, "%s_%i.xls", file_name1,x);

                /*open output file*/
                if((fp = fopen(file_name2,"w"))==NULL)
                {
                        printf("\n\nCannot open file \n");
                        exit(1);
                }

                /*print data to file*/
                fprintf(fp,"File: %s\nNumber of lineages generated:
%i",file_name2,lin);
                fprintf(fp,"\nNumber of time steps: %i\nInitial origination rate:
%.2f",chop,o_rate);
                fprintf(fp,"\nInitial extinction rate: %.2f\nEquilibrium diversity:
%i",e_rate,eqdiv);
                fprintf(fp,"\nMass extinctions = %c\n\nSampling rate:
%.2f",mass,s_rate);
                fprintf(fp,"\n'Pull of the recent' = %c\nAncestors included =
%c",pull,anc_on);
                fprintf(fp,"\nSingletons included in diversity counts = %c", sin);
                fprintf(fp,"\n\n\tComplete r2\tPartial r2");
                fprintf(fp,"\nUncorrected\t%.2f\t%.2f",r2_ud,par_r2_ud);
                fprintf(fp,"\nCorrected\t%.2f\t%.2f",r2_cd,par_r2_cd);


        fprintf(fp,"\n\nStep\tRD\tRD_dtr\tUD\tUD_dtr\tUD_mag\tCD\tCD_dtr\tCD_mag\n");

                for(s=0;s<=chop;s++)
                {

        fprintf(fp,"%i\t%i\t%.2f\t%i\t%.2f\t",s,step[s].rd,step[s].rd_dtr,step[s].ud,st
ep[s].ud_dtr);

        fprintf(fp,"%i\t%i\t%.2f\t%i\n",step[s].ud_mag,step[s].cd,step[s].cd_dtr,step[s
].cd_mag);
                }

                /*close file*/
                fclose(fp);

                /*print statistical results to master file*/

        fprintf(mfp,"%s\t%i\t%i\t%.2f\t%.2f\t%i\t",file_name2,lin,chop,o_rate,e_rate,eq
div);
                fprintf(mfp,"%c\t%.2f\t%c\t%c\t%c\t",mass,s_rate,pull,anc_on,sin);

        fprintf(mfp,"%i\t%i\t%.2f\t%.2f\t",mag_max_ud,mag_min_ud,r2_ud,par_r2_ud);
```

```
fprintf(mfp,"%i\t%i\t%.2f\t%.2f\n",mag_max_cd,mag_min_cd,r2_cd,par_r2_cd);

        printf("\nResults have been output as file %s", file_name2);

        /*FREE MEMORY*/
        free_memory(root,0);

        printf("\n\nRun another analysis on this phylogeny? y/n: ");
        scanf(" %c", &next_run);


}
while(next_run=='y');

/*close master file*/
        fclose(mfp);

        printf("\n\nStatistical results have been output to master file
%s",mfile_name);

        printf("\n\nPress any key to free memory and exit\n");
        getch();

        /*FREE MASTER TREE MEMORY*/
        free_memory(m_root,0);

        return 0;

}

/*FUNCTION DEFINITIONS*/

/*function to create a taxon node*/
taxon_t *create_taxon(taxon_t *anc, int first, int last, int gen)
{
        /*declare temporary taxon structure pointer*/
        taxon_t *temp;

/*allocate memory for new taxon node*/
if((temp=(taxon_t *)malloc(sizeof(taxon_t)))==NULL)
{
        printf("Not enough memory\n");
        exit(1);
}

/*initialise temp taxon*/
/*de-reference id pointer to assign id number to taxon*/
temp->id = *id;
/*set generation number*/
temp->gen = gen;
/*set first appearance data to current time step*/
temp->af = first;
/*set last appearance data to end of run time*/
temp->al = last;
/*initialise sampled and phylogenetic first and last*/
temp->sf = temp->pf = temp->sl = temp->pl = 0;
/*set ancestor to parent taxon address*/
temp->anc = anc;
/*set all other pointers to NULL*/
temp->d1 = temp->d2 = temp->sis = NULL;
        return temp;
}

/*recursive function to grow tree*/
void grow_tree(taxon_t *current, int step, int chop, float o_rate, float e_rate, int
eqdiv)
{
        taxon_t *d1,*d2;
        double rn;
        float orig_rate;

        /*if the current taxon does not exist (i.e. is a NULL address) return to
calling function*/
        if(current==NULL)
        {
```

```
                return;
        }


        /*if the current taxon is not extinct, and is not a newly created taxon in this
time step*/
        if(current->al==chop && current->af!=step)
        {
                /*get random number*/
                rn = RanrotA();

                /*get origination rate*/
                orig_rate = get_origination_rate(o_rate,e_rate,eqdiv);

                /*if random number is less than origination rate*/
                if(rn <= orig_rate)
                {
                        /*create descendent taxon 1, with new id.*/
                        *id = *id+1;
                        d1 = current->d1 = create_taxon(current, step, chop, current-
>gen+1);
                        /*create descendent taxon 2, with new id, set last taxon to this
descendent*/
                        *id = *id+1;
                        d2 = current->d2 = create_taxon(current, step, chop, current-
>gen+1);
                        /*set two sister pointers*/
                        d1->sis = d2;
                        d2->sis = d1;

                        /*increase last generation*/
                        if(current->gen+1>last_gen)
                        {
                                last_gen = current->gen+1;
                        }

                        /*set current taxon's extinction time to time step*/
                        current->al = step;
                        /*add one to standing diversity (two new daughters minus one
extinct parent)*/
                        *stdiv = *stdiv+1;
                }
                else
                {
                        /*get random number*/
                        rn = RanrotA();

                        /*if random number is less than extinction rate*/
                        if(rn <= e_rate)
                        {
                                /*set current taxon's extinction time to time step*/
                                current->al = step;

                                /*reduce standing diversity by one. If this reduces
diversity to zero, end program*/
                                *stdiv = *stdiv-1;
                                if(*stdiv == 0)
                                {
                                        printf("\nPhylogeny extinct before reaching
desired number of lineages.\n\n");
                                        printf("Press key to end program\n\n");
                                        getch();
                                        exit(1);
                                }
                        }
                }
        }

        /*repeat function for descendent taxa*/
        grow_tree(current->d1, step, chop, o_rate, e_rate, eqdiv);
        grow_tree(current->d2, step, chop, o_rate, e_rate, eqdiv);

        return;
}
```

```
/*recursive function to print tree*/
void print_tree(taxon_t *current, int corr)
{
	if(current!=NULL)
	{
		if(!corr)
		{
			printf("%i\t%i\t%i\t%i\t%i\n",current->id,current->af,current-
>al,current->sf,current->sl);
		}
		else
		{
			printf("%i\t%i\t%i\n",current->id,current->pf,current->pl);
		}
		print_tree(current->d1, corr);
		print_tree(current->d2, corr);
	}
	return;
}

/*recursive function to sample diversity*/
void sample_taxa(taxon_t *current,int step,int chop,char pull,char anc_on, float
s_rate)
{
	double rn;

	if(current==NULL)
	{
		return;
	}

	/*if taxon is alive*/
	if(step>=current->af && step<=current->al)
	{
		/*if ancestors are on OR it is a terminal taxon*/
		if(anc_on=='y' || current->d1==NULL)
		{
			/*get random number*/
			rn = RanrotA();

			/*if the taxon is to be sampled*/
			if(rn <= s_rate || (step==chop && pull=='y'))
			{
				/*if the first sampled appearance is not yet set*/
				if(current->sf==0)
				{
					/*set sampled first and both last appearances to
time step*/

					current->sf = current->sl = current->pl = step;
					/*if this is the final time step, set both last
appearances to step+1,

					i.e. the future, taxon is counted as 'alive'*/
					if(step==chop)
					{
						current->sl = current->pl = chop+1;
					}
					/*set last taxon*/
					last = current;
				}
				else
				{
					/*if this is the final time step, set both last
appearances to step+1,

					i.e. the future, taxon is counted as 'alive'*/
					if(step==chop)
					{
						current->sl = current->pl = chop+1;
					}
					else
					{
						/*move last appearances to time step*/
						current->sl = current->pl = step;
					}
				}
			}
		}
	}
```

```
        }

        /*repeat for descendent taxa*/
        sample_taxa(current->d1,step,chop,pull,anc_on,s_rate);
        sample_taxa(current->d2,step,chop,pull,anc_on,s_rate);

        return;
}


/*recursive function to count diversity*/
void count_taxa(taxon_t *current, int step, int *count1, int *count2, int corr, char
sin)
{
        if(current==NULL)
        {
                return;
        }


        /*if summing uncorrected data*/
        if(!corr)
        {

                /*Check actual range RUNS THROUGH this time step*/
                if(current->af<=step && current->al>=step+1)
                {
                        /*add one to diversity count 1*/
                        *count1 = *count1+1;

                        /*check that sampled range RUNS THROUGH this time step*/
                        if(current->sf<=step && current->sl>=step+1)
                        {
                                /*add one to diversity count 2*/
                                *count2 = *count2+1;
                        }
                        else
                        {
                                /*check if taxon is a singleton and singletons are
included*/
                                if(current->sf==current->sl && sin=='y')
                                {
                                        /*check if taxon is valid for inclusion in this
time step's count*/
                                        /*i.e. if its sampled first equals step AND its
actual range runs through,
                                        OR if its sampled first equals step+1 AND it goes
extinct at step+1*/
                                        if((current->sf==step && current->al>=step+1) ||
(current->sf==step+1 && current->al==step+1))
                                        {
                                                /*add one to diversity count 2*/
                                                *count2 = *count2+1;
                                        }
                                }
                        }

                }
        }

        /*if summing corrected data*/
        else
        {
                /*check that phylogenetic range RUNS THROUGH this time step*/
                if(current->pf<=step && current->pl>=step+1)
                {
                        /*add one to diversity count 2*/
                        *count2 = *count2+1;
                }
                else
                {
                        /*check if taxon is a singleton and singletons are included, and
that it
                        is not a ghost taxon (singleton ghosts never included in
count)*/
                        if(current->pf==current->pl && sin=='y' && current->d1==NULL)
                        {
```

```
step's count*/                          /*check if taxon is valid for inclusion in this time
range runs through,                     /*i.e. if its sampled first equals step AND its actual
extinct at step+1*/                     OR if its sampled first equals step+1 AND it goes
                                        if((current->pf==step && current->al>=step+1) ||
(current->pf==step+1 && current->al==step+1))
                                        {
                                                /*add one to diversity count 2*/
                                                *count2 = *count2+1;
                                        }
                        }
                }
        }

        /*repeat function for descendent taxa*/
        count_taxa(current->d1, step, count1, count2, corr, sin);
        count_taxa(current->d2, step, count1, count2, corr, sin);


        return;

}

/*postorder recursive function to free all memory used by tree*/
void free_memory(taxon_t *current, int snap)
{
        if(current==NULL)
        {
                return;
        }

        /*move to descendent taxa*/
        free_memory(current->d1,snap);
        free_memory(current->d2,snap);

        /*on return from descendent taxa, free up memory*/
        if(snap==0)
        {
                free(current);
                return;
        }

        /*if snap==1, only free memory if the taxon is not sampled*/
        if(current->sf==0)
        {

                /*set the link from taxon's ancestor to taxon to NULL. This stops
attempted later access
                of this memory block from the ancestor*/
                if(current->anc->d1==current)
                {
                        current->anc->d1=NULL;
                }
                if(current->anc->d2==current)
                {
                        current->anc->d2=NULL;
                }

                /*free memory*/
                free(current);

        }

        return;
}


/*recursive function to set ghost ranges*/
void set_ghost_range(taxon_t *current)
{

        taxon_t *relative, *ghost, *oldest, *temp_anc;
```

```
/*check for taxon non-existence*/
if(current == NULL)
{
        return;
}


/*CHECK TAXON VALID FOR MATCHING
/*check taxon is sampled and does not have a phylogenetic range set*/
if(current->sf!=0 && current->pf==0)
{

        /*FIND NEAREST UNMATCHED RELATIVE*/
        /*return relative's address. NULL if no other sampled taxa*/
        relative=find_relative(current);

        /*if no other sampled or unmatched taxa are present in the phylogeny*/
        if(relative==NULL)
        {
                /*set taxon's phylogenetic first equal to its sampled first*/
                current->pf = current->sf;
                /*set taxon's ancestor to NULL*/
                current->anc = NULL;
                /*set this taxon as the root of the new tree*/
                root = current;
                return;
        }

        /*DOES RELATIVE HAVE A NEARER RELATIVE OF ITS OWN?*/
        if(find_relative(relative)!=current)
        {
                /*repeat function for relative*/
                set_ghost_range(relative);
                return;
        }

        /*SISTERS MATCHED - Once an unmatched relative is found*/

                /*BREAK LINKS*/

                /*break the descendent links of sisters, if they are not newly created
ghost taxa*/
                /*free memory of unsampled descendents*/
                if(current->af!=0)
                {
                        free_memory(current,1);
                        current->d1=current->d2=NULL;
                }
                if(relative->af!=0)
                {
                        free_memory(relative,1);
                        relative->d1=relative->d2=NULL;
                }

                /*set sister pointers*/
                current->sis = relative;
                relative->sis = current;


                /*CREATE ANCESTRAL GHOST TAXON, INSERT INTO PHYLOGENY, BREAK OLD
LINKS*/
                *id = *id+1;
                ghost = create_taxon(NULL,0,0,0);

                /*set the two matched sisters to be the new taxon's descendents*/
                ghost->d1 = current;
                ghost->d2 = relative;


                /*get whichever sister is of the oldest generation*/
                if(current->gen<=relative->gen)
                {
                        oldest=current;
                }
                else
                {
```

```
                oldest=relative;
        }

        /*set oldest's ancestor as ghost's temporary ancestor*/

        /*if temp_anc==NULL (i.e. at root of tree) set ranges, new root and
RETURN*/
        if((ghost->anc = temp_anc = oldest->anc)==NULL)
        {
                /*set phylogenetic ranges of matched sisters*/
                if(current->sf<=relative->sf)
                {
                        relative->pf = current->pf = current->sf;

                }
                else
                {
                        relative->pf = current->pf = relative->sf;
                }

                /*set ghost's ranges to equal the start of current's range*/
                ghost->pl = ghost->pf = ghost->sl = ghost->sf = current->pf;

                /*set the new ghost taxon as the ancestor of the matched
sisters*/
                current->anc = relative->anc = ghost;

                /*set new root*/
                root = ghost;
                return;
        }


        /*set ghost's generation*/
        ghost->gen = temp_anc->gen+1;

        /*set ghost's sister*/
        /*find out which descendent of temp, oldest is. Replace with new ghost
taxon*/
        if(temp_anc->d1==oldest)
        {
                temp_anc->d1=ghost;

                /*look at temp_anc's other descendent*/
                /*if it is not already NULL*/
                if(temp_anc->d2!=NULL)
                {
                        /*If does not equal, or is not ancestral to
                        oldest's new sister, set as sister to ghost*/
                        if(temp_anc->d2!=oldest->sis && find_relative(temp_anc-
>d2)!=oldest->sis)
                        {
                                ghost->sis=temp_anc->d2;
                        }
                        else
                        {
                                /*free memory of temp_anc's d2 unsampled
descendents*/
                                free_memory(temp_anc->d2,1);
                                /*break link to other descendent, leave ghost's
sister as NULL*/
                                temp_anc->d2=NULL;
                        }
                }

        }
        else
        {
                temp_anc->d2=ghost;

                /*look at temp_anc's other descendent/*
                /*if it is not already NULL*/
                if(temp_anc->d1!=NULL)
                {
                        /*If it does not equal, or is not ancestral to
                        oldest's new sister, set as sister to ghost*/
```

```
>d1)!=oldest->sis)
                        if(temp_anc->d1!=oldest->sis && find_relative(temp_anc-
                        {
                                ghost->sis=temp_anc->d1;
                        }
                        else
                        {
                                /*free memory of temp_anc's d1 unsampled
descendents*/
                                free_memory(temp_anc->d1,1);
                                /*break link to other descendent, leave ghost's
sister as NULL*/
                                temp_anc->d1=NULL;
                        }
                }
        }

/*set phylogenetic ranges of matched sisters*/
if(current->sf<=relative->sf)
{
        relative->pf = current->pf = current->sf;

}
else
{
        relative->pf = current->pf = relative->sf;
}

/*set ghost's pl and sf, sl to equal the start of current's range*/
ghost->pl = ghost->sl = ghost->sf = current->pf;

/*set the new ghost taxon as the ancestor of the matched sisters*/
current->anc = relative->anc = ghost;

}

/*move onto ancestor*/
set_ghost_range(current->anc);
        return;
}


/*function to find nearest sampled relative*/
taxon_t *find_relative(taxon_t *current)
{
        taxon_t *start, *relative;
        int gen;


        /*run through all descendents, until last generation is reached*/
        for(gen=current->gen;gen<=last_gen;gen++)
        {
                /*call recursive function to call relatives, check if they are sampled,
and of
                the correct generation, NULL returned if no sampled relatives are
found*/
                relative=search(current,gen);

                /*if a sampled relative is found, stop searching,*/
                /*unless the relative is the current taxon!*/
                if(relative!=NULL && relative!=current)
                {
                        return relative;
                }
        }

        /*start a loop looking through taxon's sister+descendents, followed by
ancestors plus
        descendents etc*/
        start = current;

        do
        {

                /*if sister is not NULL, validate sister and descendents*/
```

```
                if(start->sis!=NULL)
                {
                        start=start->sis;

                        /*run through all generations, until last generation is
reached*/
                        for(gen=start->gen;gen<=last_gen;gen++)
                        {

                                /*call recursive function to call relatives of this
generation, check if
                                they are sampled, NULL returned if no sampled relatives
are found*/
                                relative=search(start,gen);
                                /*if a sampled relative is found, stop searching,*/
                                /*unless the relative is the current taxon!*/
                                if(relative!=NULL && relative!=current)
                                {
                                        return relative;
                                }
                        }

                }

                /*set start and relative to ancestor, to go back through the loop*/
                /*if ancestor==NULL, i.e. at root, return NULL*/
                if((start=relative=start->anc)==NULL)
                {
                        return NULL;
                }

        }
        /*loop while relative is not sampled or while relative is the current taxon*/
        while(relative->sf==0 || relative==current);

        return relative;

}

/*postorder recursive function to check relatives for being sampled and unmatched*/
taxon_t *search(taxon_t *current, int gen)
{
        /*declare relative taxon, NULL as default. Declare temp taxon*/
        taxon_t *relative=NULL, *temp;

        if(current==NULL)
        {
                return NULL;
        }

        /*if the current taxon is sampled, unmatched, and it is of the correct
generation*/
        if(current->sf!=0 && current->pf==0 && current->gen==gen)
        {
                return current;
        }

        /*if current taxon is not sampled or of the correct generation, move onto d1
taxon*/
        temp=search(current->d1,gen);

        /*if function returns a valid taxon, set relative to this taxon*/
        if(temp!=NULL)
        {
                relative=temp;
        }

        /*move onto d2 taxon*/
        temp=search(current->d2,gen);

        if(temp!=NULL)
        {
                relative=temp;
        }
```

```
        return relative;
}


float get_origination_rate(float o_rate, float e_rate, int eqdiv)
{
        /* if diversification is exponential, or if a mass extinction event is
occurring*/
        if(eqdiv == 0 || e_rate == mass_rate)
        {
                return o_rate;
        }

        /*else if diversification is logistic*/

        /*Algorithm for calculating diversity dependent origination rate*/
        /*reduce the difference between rates by the same proportion as standing
diversity to eq diversity*/
        /*o_rate = o_rate - ((o_rate-e_rate)*(*stdiv/eqdiv)). Rearranged:*/
        o_rate = o_rate - *stdiv*((o_rate-e_rate)/eqdiv);

        return o_rate;

}

/*function to create duplicate phylogeny*/
void copy_tree(taxon_t *copy, taxon_t *master)
{

        if(master == NULL)
        {
                return;
        }


        /*copy all data*/
        copy->id = master->id;
        copy->gen = master->gen;
        copy->af = master->af;
        copy->al = master->al;

        /*if not at terminal branch of tree, create two daughters for copy*/
        if(master->d1 != NULL)
        {
                copy->d1 = create_taxon(copy,0,0,0);
                copy->d2 = create_taxon(copy,0,0,0);

                copy->d1->sis = copy->d2;
                copy->d2->sis = copy->d1;

        }

        /*move onto daughters*/
        copy_tree(copy->d1, master->d1);
        copy_tree(copy->d2, master->d2);

        return;

}

/*function to get r2, the product-moment correlation coefficient*/
float get_correlation_coefficient(int n,float sum_xy,float sum_x,float sum_y,float
sum_x2,float sum_y2)
{
        float r;
        float r2;

        r = ((n*sum_xy)-(sum_x*sum_y))/sqrt(((n*sum_x2)-(sum_x*sum_x))*((n*sum_y2)-
(sum_y*sum_y)));
        r2 = r*r;
        return r2;
}

/*RANROT random number generator*/

/* returns a random number between 0 and 1 */
double RanrotA() {
```

```
  my_uint x;
  /* generate next random number */
  x = randbuffer[r_p1] = rotl(randbuffer[r_p2], R1) + rotl(randbuffer[r_p1], R2);
  /* rotate list pointers */
  if (--r_p1 < 0) r_p1 = KK - 1;
  if (--r_p2 < 0) r_p2 = KK - 1;
  /* conversion to float */
  return x * scale;}

/* this function initializes the random number generator.      */
/* Must be called before the first call to RanrotA or iRanrotA */
void RanrotAInit (my_uint seed) {
  int i;

  /* put semi-random numbers into the buffer */
  for (i=0; i<KK; i++) {
    randbuffer[i] = seed;
    seed = rotl(seed,5) + 97;}

  /* initialize pointers to circular buffer */
  r_p1 = 0;  r_p2 = JJ;

  /* randomize */
  for (i = 0;  i < 300;  i++) RanrotA();

  /* compute 2^(- integer size) */
  scale = ldexp(1, -8*sizeof(my_uint));
}
```

GHOSTRANGE_B alternative code for inserting a ghost lineage between descendent and ancestor:

```
/*set phylogenetic ranges of matched sisters*/
/*if not direct ancestor-descendents*/
if(dir_anc == 0)
{
        if(current->sf<=relative->sf)
        {
                relative->pf = current->pf = current->sf;

        }
        else
        {
                relative->pf = current->pf = relative->sf;
        }

        /*set ghost's ranges to equal the start of current's range*/
        ghost->pl = ghost->sl = ghost->sf = current->pf;
}

/*if direct ancestor-descendent*/
else
{
        /*if current is the ancestor*/
        if(current->gen<relative->gen)
        {
                /*set relative's phylogenetic first equal to current's
sampled LAST*/
                relative->pf = current->sl;
                /*set current's phylogenetic first equal to its sampled
first*/
                current->pf = current->sf;

                /*set ghost's ranges to equal the start of current's
range*/
                ghost->pl = ghost->sl = ghost->sf = current->pf;

        }
        /*if relative is the ancestor*/
        else
        {
```

```
                                        /*set current's phylogenetic first equal to relative's
sampled LAST*/
                                        current->pf = relative->sl;
                                        /*set relative's phylogenetic first equal to its sampled
first*/
                                        relative->pf = relative->sf;

                                        /*set ghost's ranges to equal the start of relative's
range*/
                                        ghost->pl = ghost->sl = ghost->sf = relative->pf;
                                }
                        }

/*function to determine if two taxa are on a direct line*/
int dir_line(taxon_t *taxon1, taxon_t *taxon2)
{
        taxon_t *temp;

        /*if taxon 1 is the youngest*/
        if(taxon1->gen>taxon2->gen)
        {
                temp = taxon1;

                /*move through ancestors trying to find match until root is reached*/
                while(temp->anc!=NULL)
                {
                        if(temp->anc == taxon2)
                        {
                                return 1;
                        }

                        temp = temp->anc;

                };

        }

        /*if taxon 2 is the youngest*/
        if(taxon2->gen>taxon1->gen)
        {
                temp = taxon2;

                /*move through ancestors trying to find match until root is reached*/
                while(temp->anc!=NULL)
                {
                        if(temp->anc == taxon1)
                        {
                                return 1;
                        }

                        temp = temp->anc;

                };
        }

        return 0;
}
```

Appendix Ib. CLOCKBACK program

The following listing is based on code written in the Q-Basic language by Paul Pearson of Bristol University.

The program is included on the IBM disc accompanying this thesis. The code is written in the C programming language, source code comments are included and are indicated by /* */.

Source code listing for the CLOCKBACK program:

```
/*C Clockback program*/

#include <stdio.h>
#include <stdlib.h>
#include <time.h>
#include <conio.h>
#include <math.h>
#include <string.h>
/* max size,(9999 taxa processed fully - 1st array row not used)*/
#define SIZE 10001

/*RANROT random number generator*/

/* define desired integer type */
typedef  unsigned int my_uint;

/* If your system doesn't have a rotate function for the chosen integer type
   then define it thus:*/
my_uint rotl (my_uint x, my_uint r) {
  return (x << r) | (x >> (sizeof(x)*8-r));}

/* define parameters (R1 and R2 must be smaller than the integer size): */
#define KK  17
#define JJ  10
#define R1   5
#define R2   3

/* global variables */
my_uint randbuffer[KK];  /* history buffer */
int r_p1, r_p2;          /* indexes into history buffer */
float scale;             /* 2^(- integer size) */

void RanrotAInit (my_uint seed);
double RanrotA();

/*Running results function*/
void run_res(int tree, int attempt, int counter, int step, int ext);
/*End results function*/
void end_res(int counter, int step, int info[SIZE][3], char file_name[31], int tree);

main()
{

        float rate, rand_no;
        int ext, counter, step, x, y, chop, min_div, min_size, tree_tot, tree;

        /*Number of tries may get very large*/
        unsigned attempt;
        /*FIRST ARRAY ROW (0) WILL NOT BE USED*/
        int info[SIZE][3];
        char file_name[31];

        printf("\n\tCLOCKBACK\n\n");

        puts("\nEnter number of successful trees you would like generated (Max 999):");
```

```
scanf(" %i", &tree_tot);
puts("\n\nEnter file name for results output (Max 30 characters, no spaces):");
scanf(" %s", file_name);
puts("\n\nChop tree after (m.yr):");
scanf(" %i", &chop);
puts("\n\nSpecify evolutionary rate (events per taxon per m.yr) e.g.0.114.:");
scanf(" %f", & rate);
puts("\n\nSpecify minimum tree size (total number of taxa):");
scanf(" %i", & min_size);
puts("\n\nSpecify minimum end diversity (number of taxa alive at end):");
scanf(" %i", & min_div);

printf("\nProgram running, please wait for output...\n\n");

/* initialize, using time as random seed */
RanrotAInit(time(0));

for(tree=1; tree<=tree_tot; tree++)
{

        ext=0;              /*initialise variables*/
        step=1;
        y=0;
        attempt=1;


        /*initialise results array*/

        for(counter=0; counter<SIZE; counter++)
        {
                for(x=0; x<3; x++)
                {
                        /*set all potential taxa extinction times to 0*/
                        info[counter][x]=0;
                }
        }

        /*set taxon 1 ext time to chop, in case it does not go extinct*/
        info[1][1]=chop;
        /*set taxa counter back to 1*/
        counter=1;



        /*loop while time limit is not up*/
        /*or total size has not reached minimum*/
        /*or end diversity has not reached minimum*/
        /*ALL these must be false for the loop to end*/
        while(step<chop || counter<min_size || counter-ext<min_div)
        {

                if(counter-ext>0 && counter<SIZE && step<chop)
                {
                /*loop while diversity does not equal zero,*/
              /*and is less than maximum limit, and time limit is not up*/
                /*ONLY ONE of these must be false for the loop to end*/

                        if(y!=counter)
                        {
                                y++;
                                /*if taxon has not yet got an ext time*/
                                if(info[y][1]==chop)
                                {

                                /*random number generation*/
                                rand_no=RanrotA();



                                if(rand_no<=rate)
                                {
                                        /*produce new taxon*/
                                        counter=counter+1;
                                        /*Record ogt time of new

taxon(counter)*/

                                        info[counter][0]=step;
```

```
tree duration (in case taxon doesn't go extinct)*/

of new taxon(counter)*/



of taxon y*/

(y=counter) increment time*/

reaching min),*/

                /*sets extinction time to

                info[counter][1]=chop;
                /*Records parent taxon(y)

                info[counter][2]=y;
        }

        /*2nd random number*/
        rand_no=RanrotA();


        if(rand_no<=rate)
        {
                ext=ext+1;
                /*Record extinction time

                info[y][1]=step;
                }
        }


        }
        else
        {
                /*when all taxa have been processed

                /*by one and start again.*/
                step=step+1;
                y=0;
        }

}


else
{
        /*if diversity hits 0 or SIZE, or chop(without

        attempt=attempt+1;
        /*increment attempt by one and start again*/
        counter=1;
        step=1;
        y=0;
        ext=0;
        /*re-set the first taxon's ext time to chop*/
        info[1][1]=chop;
}


}

run_res(tree,attempt,counter,step,ext);

end_res(counter, step, info, file_name, tree);

}

printf("\n\nResults have been output as files %s1.xls - %s%i.xls.\n",
file_name, file_name, tree_tot);

printf("\nPress any key to end program\n");

getch();

return 0;
}

/*RANROT random number generator*/

/* returns a random number between 0 and 1 */
double RanrotA() {
  my_uint x;
  /* generate next random number */
  x = randbuffer[r_p1] = rotl(randbuffer[r_p2], R1) + rotl(randbuffer[r_p1], R2);
  /* rotate list pointers */
```

```
  if (--r_p1 < 0) r_p1 = KK - 1;
  if (--r_p2 < 0) r_p2 = KK - 1;
  /* conversion to float */
  return x * scale;}

/* this function initializes the random number generator.      */
/* Must be called before the first call to RanrotA or iRanrotA */
void RanrotAInit (my_uint seed) {
  int i;

  /* put semi-random numbers into the buffer */
  for (i=0; i<KK; i++) {
    randbuffer[i] = seed;
    seed = rotl(seed,5) + 97;}

  /* initialize pointers to circular buffer */
  r_p1 = 0;  r_p2 = JJ;

  /* randomize */
  for (i = 0;  i < 300;  i++) RanrotA();

  /* compute 2^(- integer size) */
  scale = ldexp(1, -8*sizeof(my_uint));
}

void run_res(int tree, int attempt, int counter, int step, int ext)
{
        printf("\nTree no: %i Attempts: %i Diversity: %i Size: %i Time:
%i",tree,attempt,counter-ext,counter,step);

        return;
}


void end_res(int counter, int step, int info[SIZE][3], char file_name[31], int tree)
{
        FILE *ofp;

        int p;
        char newfile_name[34];

        sprintf(newfile_name, "%s%i.xls", file_name, tree);



        if((ofp = fopen(newfile_name,"w"))==NULL)
        {
                printf("\n\nCannot open file \n");
                exit(1);
        }

        fprintf(ofp,"Taxon no.\tFAD\tLOD\tRange\tAncestor I.D.");


        for(p=1; p<=counter; p++)
        {
                /*invert ogt/ext times*/
                info[p][0]=step-info[p][0];
                info[p][1]=step-info[p][1];
                fprintf(ofp,"\n%i\t%i\t%i\t%i\t%i",p,info[p][0],info[p][1],info[p][0]-
info[p][1],info[p][2]);
        }

        fclose(ofp);

        return;
}
```

Appendix Ic. ADAPTS program

The following listing is based on the diversity metrics calculation functions of the ADAPTS program, written in the Q-Basic language by Al McGowan of the University of Chicago. For Q-Basic source code see McGowan and Pearson (1999).

The program is included on the IBM disc accompanying this thesis. The code is written in the C programming language, source code comments are included and are indicated by /* */.

Source code listing for ADAPTS:

```
/*ADAPTS program*/

#include <stdio.h>
#include <stdlib.h>
#include <conio.h>

#define SIZE 10000

/*Functions list*/

float diversity_calc(float input[SIZE][4], int taxa_no, int interval, float timestep);
float ogts_calc(float input[SIZE][4],int taxa_no,int interval,float timestep);
float exts_calc(float input[SIZE][4],int taxa_no,int interval,float timestep);
float r_ogt(float diversity,float ogts,float timestep);
float r_ext(float diversity,float exts,float timestep);
int file_output(float output[SIZE][8], float start, float timestep, float slots, char
file_name[31]);


main()
{

        /*discard string for header row, and file name string*/
        char dis_str[300], file_name[31];
        /*discard variable for tabs and new lines in dataset*/
        char trash;
        /*discard variable for taxa no.*/
        int trash1;
        /*counters for use in loops*/
        int counter,slots_no,taxa_no,interval;
        /*initial parameters*/
        float taxa,timestep,start,end,slots;
        /*diversity metrics*/
        float diversity=0,ogts=0,exts=0,ro,re;
        /*array for data input. Maximum of 9999 taxa can be input*/
        float input[SIZE][4];
        /*array for data output. Maximum of 9999 timeslots*/
        float output[SIZE][8];
        /*File pointer*/
        FILE *ofp;

        printf("Enter name of datafile to be processed, including file extension,
.xls/.txt.\n");
        printf("(Max. 30 characters, no spaces. Data must be in text(tab delimited)
format):\n\n");
        scanf(" %s", file_name);
        printf("\nEnter number of taxa (max 10000):\n\n");
        scanf(" %f", &taxa);
        /*calculation interval e.g. 1 m.yr, 10 m.yr*/
        printf("\nSet calculation interval\n");
        printf("(must divide exactly into the total time range):\n\n");
        scanf(" %f", &timestep);
        /*start point e.g. 500 myr ago*/
```

```
printf("\nSet analysis start point:\n\n");
scanf(" %f", &start);
/*end point e.g. 0 myr ago*/
printf("\nSet analysis end point:\n\n");
scanf(" %f", &end);

slots=(start-end)/timestep;   /*number of calculation intervals*/


if((ofp=fopen(file_name,"r"))==NULL)
{
                /*open file, return error message if*/
                /*unsuccessful*/
                printf("Error opening file\n");
                printf("\nPress any key to end program\n\n");
                getch();
                exit(1);
        }

        /*Reads the header line into a discard string*/
        fgets(dis_str,300,ofp);

        /*not using first array row*/
        /*data input, from file into array*/
        for(counter=1; counter<=taxa; counter++)
        {

                fscanf(ofp,"
%i%c%f%c%f%c%f%c%f%c",&trash1,&trash,&input[counter][0],&trash,&input[counter][1],&tra
sh,&input[counter][2],&trash,&input[counter][3],&trash);
        }

        fclose(ofp);


        /*Calculate diversity metrics for each timestep interval*/

        /*loop for each interval*/
        /*Won't give an output for interval=0*/
        /*i.e. last interval processed will end at 0*/
        for(slots_no=0; slots_no<slots; slots_no++)


        {
                interval=start-(timestep*slots_no);  /*set interval for this loop*/
                diversity=0;
                ogts=0;
                exts=0;


                /*Diversity, originations, extinctions functions*/

                for(taxa_no=1; taxa_no<=taxa; taxa_no++)  /*loop for each taxon*/
                {

                        diversity = diversity +
diversity_calc(input,taxa_no,interval,timestep);
                        ogts = ogts + ogts_calc(input,taxa_no,interval,timestep);
                        exts = exts + exts_calc(input,taxa_no,interval,timestep);

                }

                /*Per-taxon rate of origination and extinction functions*/

                ro = r_ogt(diversity,ogts,timestep);
                re = r_ext(diversity,exts,timestep);

                /*Output results to the array row of this interval*/

                output[interval][0]=diversity;          /*standing diversity*/
                output[interval][1]=ogts;               /*no. of originations*/
                output[interval][2]=exts;               /*no. of extinctions*/
                output[interval][3]=ro;                 /*per-taxon rate of
origination*/
                output[interval][4]=re;                 /*per-taxon rate of
extinction*/
```

```
                output[interval][5]=ro-re;                  /*rate of diversification*/
                output[interval][6]=ro+re;                  /*rate of turnover*/
                output[interval][7]=diversity*(ro-re);      /*change in diversity*/

        }   /*End of 'slots' for-loop*/


    return file_output(output,start,timestep,slots,file_name);



}

/*DIVERSITY CALCULATION FUNCTION*/

float diversity_calc(float input[SIZE][4], int taxa_no, int interval, float timestep)
{
        /*if some part of taxon's range is within interval*/
        if(input[taxa_no][0]>interval-timestep && input[taxa_no][1]<interval)
        {
                /*if fad of taxon is on or after the interval start*/
                if(input[taxa_no][0]<=interval)
                {
                        /*if lod is before interval end*/
                        if(input[taxa_no][1]>interval-timestep)
                        {

                                /*return proportion of interval taxon is present for*/
                                return (input[taxa_no][0]-input[taxa_no][1])/timestep;
                        }

                        /*if lod of taxon is on or after interval end*/
                        else
                        {
                                /*return proportion of interval taxon is present for*/
                                return (input[taxa_no][0]-(interval-timestep))/timestep;
                        }
                }

                 /*if fad of taxon is before interval start*/
                else
                {
                        /*if lod of taxon is on or after interval end*/
                        if(input[taxa_no][1]<=interval-timestep)
                        {

                                /*return 1: taxon is present throughout interval*/
                                return 1;
                        }

                        /*if lod of taxon is before interval end*/
                        else
                        {
                                /* return proportion of interval taxon is present for*/
                                return (interval-input[taxa_no][1])/timestep;
                        }
                }

                /*if no part of taxon's range is within interval*/
                else
                {
                        return 0;
                }
}


/*ORIGINATIONS CALCULATION FUNCTION*/

float ogts_calc(float input[SIZE][4],int taxa_no,int interval,float timestep)
{
        /*if taxon fad falls within interval*/
```

```
        /*(but not on lower boundary)*/
        if(input[taxa_no][0]<=interval && input[taxa_no][0]>interval-timestep)
        {
                return 1;
        }
        else
        {
                return 0;
        }
}


/*EXTINCTIONS CALCULATION FUNCTION*/

float exts_calc(float input[SIZE][4],int taxa_no,int interval,float timestep)
{
        /*if taxon lod falls within interval*/
        /*(but not on upper boundary), and is not 0 (still alive)*/
        if(input[taxa_no][1]<interval && input[taxa_no][1]>=interval-timestep &&
input[taxa_no][1] != 0)
        {
                return 1;
        }
        else
        {
                return 0;
        }
}

/*PER-TAXON RATE OF ORIGINATION FUNCTION*/

float r_ogt(float diversity,float ogts,float timestep)
{
        if(diversity==0)
        {
                return 0;
        }
        else
        {
                return (ogts/timestep)*(1/diversity);
        }
}

/*PER-TAXON RATE OF EXTINCTION FUNCTION*/

float r_ext(float diversity,float exts,float timestep)
{
        if(diversity==0)
        {
                return 0;
        }
        else
        {
                return (exts/timestep)*(1/diversity);
        }
}


/*RESULTS OUTPUT FUNCTION*/

int file_output(float output[SIZE][8], float start, float timestep, float slots, char
file_name[31])
{
        FILE *ofp;


        int p,intl;


        if((ofp = fopen(file_name,"a"))==NULL)
        {
                printf("\n\nCannot open file \n");
                exit(1);
        }
```

```
        fprintf(ofp,"\nTime\tDiversity\tOriginations\tExtinctions\tro\tre\trd\trt\tRate
of change in diversity");

        /*loop for each interval*/
        for(p=0; p<slots; p++)

        {
                /*set interval to be output*/
                intl=start-(timestep*p);

                /*print output to file*/
                fprintf(ofp,"\n %i \t %.5f \t %f \t
%f",intl,output[intl][0],output[intl][1],output[intl][2]);
                fprintf(ofp,"\t %.5f \t %.5f \t %.5f \t %.5f \t
%.5f",output[intl][3],output[intl][4],output[intl][5],output[intl][6],output[intl][7])
;
        }

        fclose(ofp);

        printf("\n\nResults have been appended to file %s.\n", file_name);

        printf("\nPress any key to end program\n\n");

        getch();

        return 0;
}
```

APPENDIX II: IBM DISC CONTENTS

IIa. Description of contents

Accompanying this thesis is a CD-ROM formatted for the IBM PC. The disc contains three directories 'TAXONOMIC', 'Programs', and 'CH2_results'. Descriptions follow of the programs and data contained within these directories. All files are compatible with Windows 98 and later operating systems.

1) TAXONOMIC database (see Chapter 3 for description). A Microsoft Access database file, size 2.1 mb. The *Fossil Record 2* (Benton 1993), and Sepkoski (1992) data compendia, with associated SQL queries, are contained within this database. The Sepkoski unpublished compendia of genera, and associated SQL queries, are not included as permission has not been given to distribute this data. SQL queries are as described in Chapter 3, Section 3.2.2.4. Any not described in that section are intermediate queries which do not require execution for a top-level query to run successfully. Upon opening the database the 'queries' window is in view. To view the data tables, click on the 'Tables' tab. To run a query or open a table, double click on the appropriate icon. To use the SQL queries for data selection and manipulation the TAXONOMIC.mdb file must be copied onto the C drive of a PC, and the 'read only' box of the file's properties menu should be unchecked. This allows the SQL code to be altered and saved. Alternatively data can be manipulated by the use of the Access program's graphical user interface.
2) Programs folder. This directory contains the GHOSTRANGE_A (225 kb), GHOSTRANGE_B (225 kb), CLOCKBACK (213 kb) and ADAPTS (193 kb) programs (see Chapters 2 and 4 for descriptions). These are DOS programs designed to run on an IBM PC. See Appendix IIb below for user instructions.
3) Chapter 2 results files. Seven Microsoft Excel spreadsheet files, combined size 223kb. These are the master files containing a summary of the defining parameters and results of all the simulated phylogenies created and sampled by the GHOSTRANGE programs for the analysis

presented in Chapter 2. The following table correlates each file on the IBM disc with its corresponding results table in Chapter 2.

Excel file name (CD_ROM)	Results table (Chapter 2)
Analysis1.xls	2.1
Analysis2.xls	2.4
Analysis3.xls	2.6
Analysis4.xls	2.7
Analysis5.xls	2.9
Analysis6.xls	2.10
Analysis7.xls	2.12

The headings used in the spreadsheet files are those output by the GHOSTRANGE programs, and are described below:

Defining parameters

- File: Excel file name of the simulated phylogeny
- Lineages: Total number of taxa created
- Time steps: Number of time steps that simulation was run for
- ko: Initial rate of origination (taxa per Lmy)
- ke: Initial rate of extinction (taxa per Lmy)
- Deq: Equilibrium diversity. A value of 0 indicates exponential diversification
- Mex: Mass extinctions simulated, yes or no
- SI: Sampling intensity (occurrences per Lmy)
- PR: 'Pull of the Recent' simulated, yes or no
- Anc: Ancestors included in analysis, yes or no
- S_tons: Singleton taxa included in analysis, yes or no.

Results

- Uncorrected and corrected diversity statistics
    - Mag(max): Maximum estimated diversity magnitude as a percentage of the real diversity magnitude
    - Mag(min): Minimum estimated diversity magnitude as a percentage of the real diversity magnitude

- r2: squared product-moment correlation coefficient of estimated diversity correlated with real diversity
- p_r2: squared partial correlation coefficient of estimated diversity correlated with real diversity.

IIIb. User instructions for programs

Below are the user instructions for the GHOSTRANGE, CLOCKBACK and ADAPTS programs. All are DOS programs with command line user interface.

GHOSTRANGE_A, GHOSTRANGE_B

The instructions for these two programs are identical, the only difference in the programs is their method of inserting ghost lineages between ancestors and descendents (see Chapter 2, Section 2.2.2).

1) Enter phylogeny generation parameters. There are five parameters to be entered, (number of lineages, origination rate, extinction rate, equilibrium diversity, mass extinctions) these are described in Chapter 2, Section 2.2.2.2.
2) Enter phylogeny file name. This is the stem name for the Excel results files. File extension is not required.
3) The phylogeny is generated. If the tree goes extinct before the desired number of lineages is reached, a message is displayed and the program ends. If the tree is successfully generated a message is displayed giving the number of lineages produced and the number of time steps taken.
4) Enter sampling and ghost lineage insertion parameters. A further four parameters must be entered (sampling rate, Pull of the Recent, Ancestors included, singletons included) to direct the program how to sample and reconstruct the phylogeny, and how to sum the resulting diversity. These are described in section 2.2.2.2.
5) Upon completion of the diversity summing, the program outputs a results file for this analysis, the file name is given on the screen. The user is then asked if another analysis is wanted on this phylogeny. If yes (y), step (4)

is repeated and a second results file is output. This continues until the user answers no (n).

6) A master file containing the generating parameters and results for all the analyses run on this phylogeny is then output, the file name is given on the screen. The program then ends.
7) All results files are output to the directory containing the GHOSTRANGE program. Individual files contain the generating parameters for the phylogeny and sampling regime, correlation coefficients (full and partial) for the correlation between the uncorrected/corrected estimates and real diversity counts, and a full listing of diversity at each time step:
   - Step: time step
   - RD: real diversity
   - RD_dtr: real diversity detrended (linear trend through time removed)
   - UD: uncorrected diversity
   - UD_dtr: uncorrected diversity detrended
   - CD: corrected diversity
   - CD_dtr: corrected diversity detrended.
8) Master file headings are as described in Appendix IIa (3) above.

CLOCKBACK

1) Enter tree generation parameters. These are the five parameters (number of trees, time length, evolutionary rate, minimum tree size, minimum end diversity) as described in Chapter 4, Section 4.2.2.2, and also include a prompt for the user to enter a stem file name for the Excel results files. File extension is not required.
2) Once the required number of trees have been generated, the program prints to the screen a summary of each tree. This information consists of the number of unsuccessful attempts required to produce the tree, the diversity of the tree in the final time step, the total size of the tree, and the number of time steps. Also printed to the screen is the range of file names of the results files.

3) Results files are output to the directory containing the CLOCKBACK program. Each results file contains the full taxonomic time range listing of each tree:
   - Taxon no.: i.d. number of the taxon
   - FAD: First appearance date
   - LOD: last occurrence date
   - Range: total time range
   - Ancestor I.D.: id number of the taxon's parent.

   This information is formatted for input into the ADAPTS program.

ADAPTS

The following user instructions are for the version of the ADAPTS program written for the IBM PC. This program contains only the diversity metrics calculation functions of the original ADAPTS program, written for the Apple Macintosh by Al McGowan of the University of Chicago. For user instructions for the Apple Mac version see McGowan and Pearson (1999).

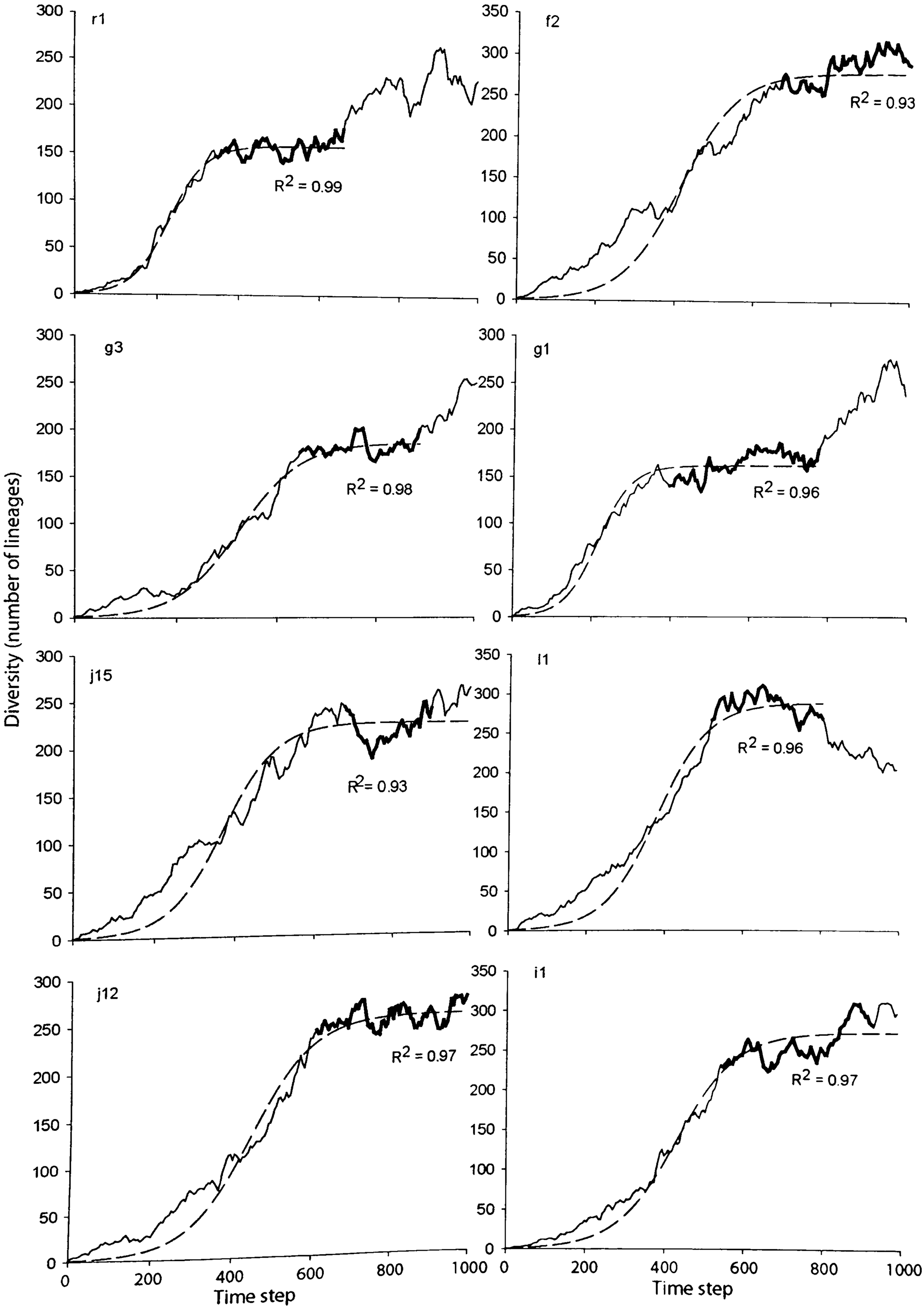
1) The file containing the taxonomic range information to be processed must be located in the same directory as the ADAPTS program. This can be a text (.txt) or Excel (.xls) file, but must be in the same format as the files output from the CLOCKBACK program, i.e. Five columns: 1. Taxon i.d. number. 2. First appearance. 3. Last occurrence. 4. Time range. 5. Ancestor i.d. number. A headings row must be included, although the exact wording of the column titles is not important, and fields must be tab delimited, i.e. a tab included between each field in a text file, or the file saved as 'text (tab delimited)' in Excel.
2) Enter file name. The exact file name must be entered, *including* the file extension (.txt or .xls).
3) Four pieces of information are entered:
   - Number of taxa in file
   - Calculation interval required, for example 5 myr, or 5 time steps. This must divide exactly into the total analysis time period

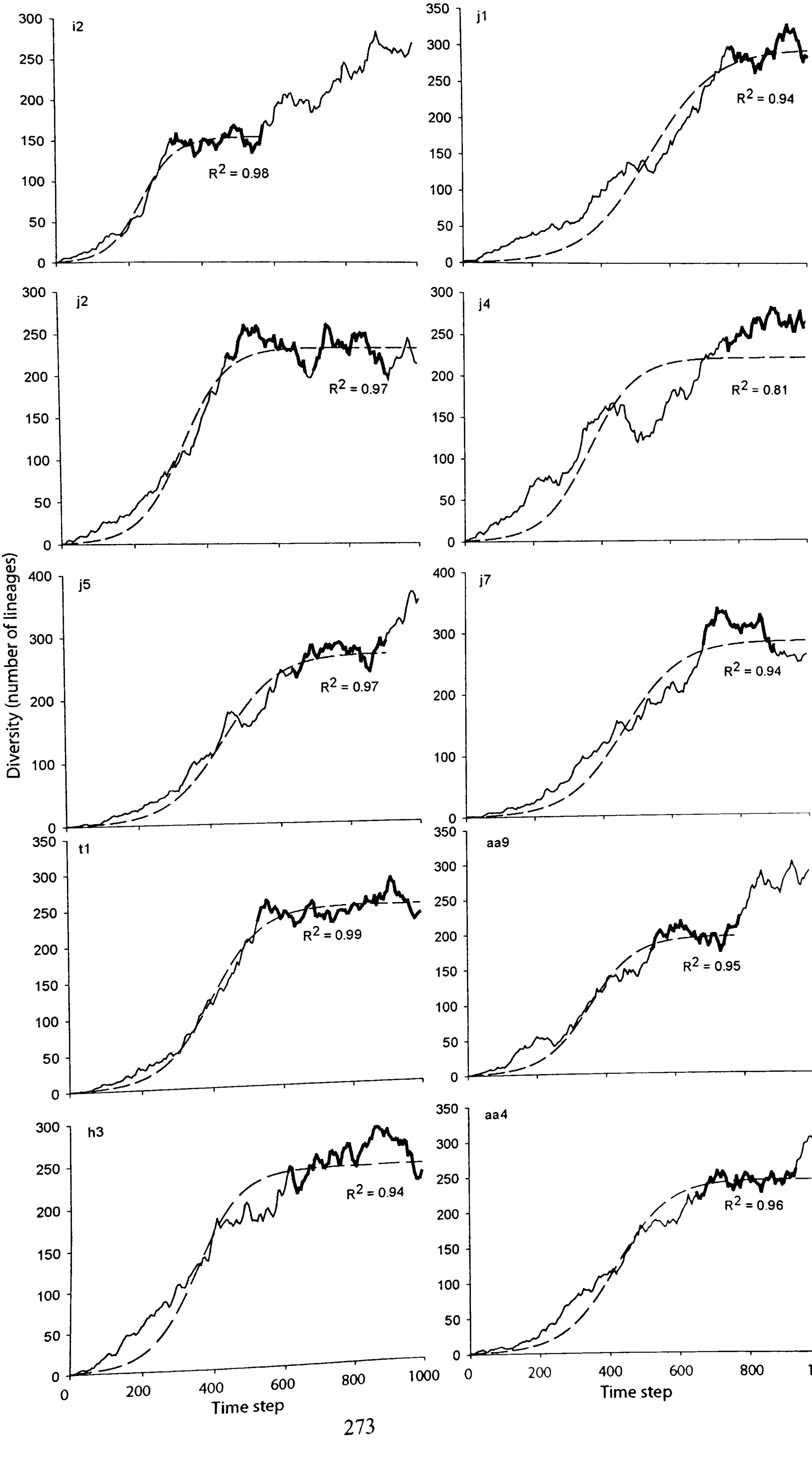
- Analysis start point. The time at which the first diversity count should be taken, e.g. 50 myr, or 50 time steps
- Analysis end point. The time at which the last diversity count should be taken, e.g. 0 myr, or 0 time steps.

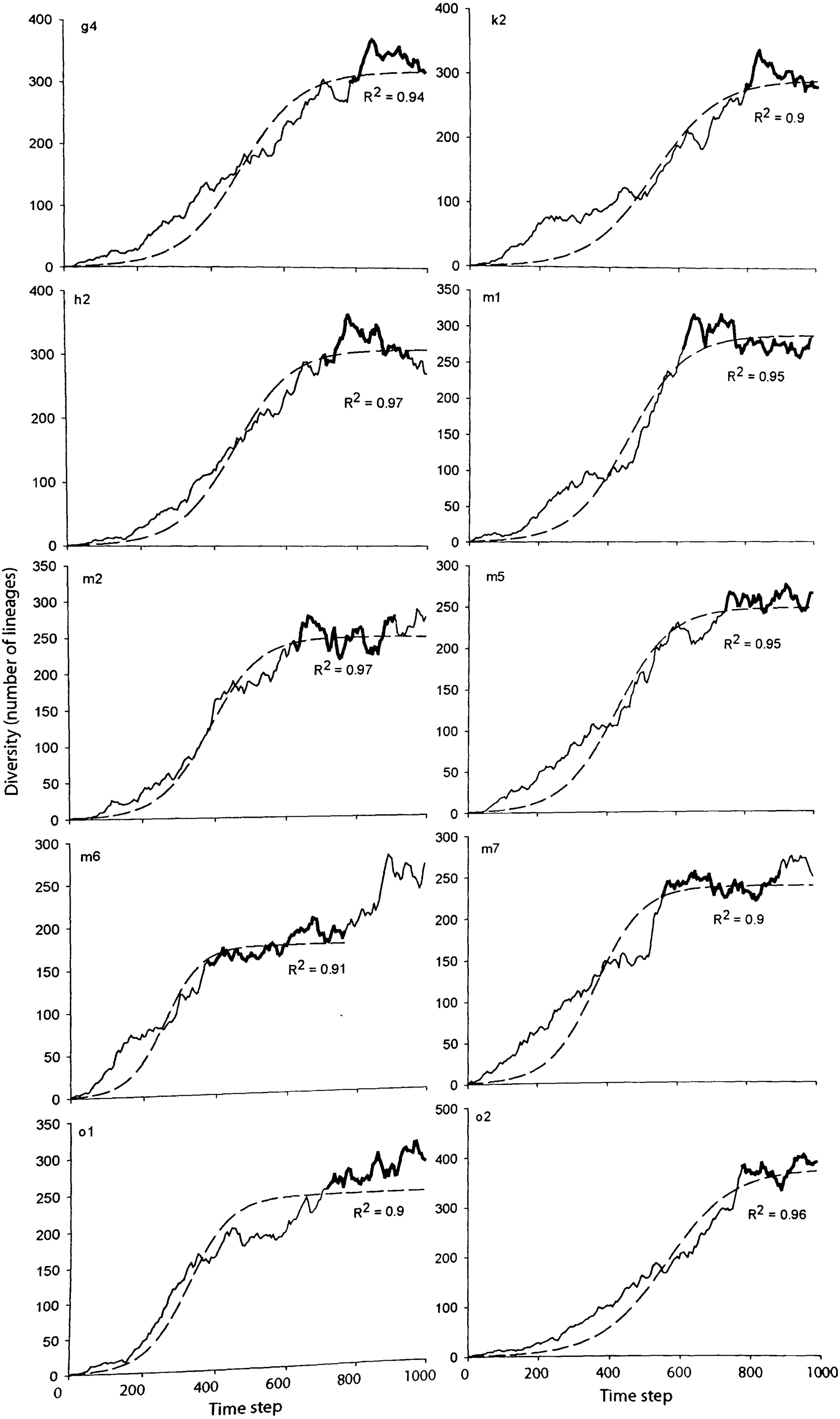
4) If the program is unable to locate the file named by the user, an error message is displayed and the program will end. If the program is able to locate the file the analysis will run and results appended onto the end of the input file.
5) The results files consist of the complete diversity metrics listing for each time interval within the analysis period:
   - Time: Time interval starting with the oldest
   - Diversity: diversity summed using the method of Wei and Kennett (1986)
   - Originations
   - Extinctions
   - ro: rate of origination (taxa per Lmy)
   - re: rate of extinction (taxa per Lmy)
   - rt: rate of turnover (taxa per Lmy)
   - rd: rate of diversification (taxa per Lmy)
   - Rate of change in diversity: rate of diversification multiplied by standing diversity (taxa per million years).

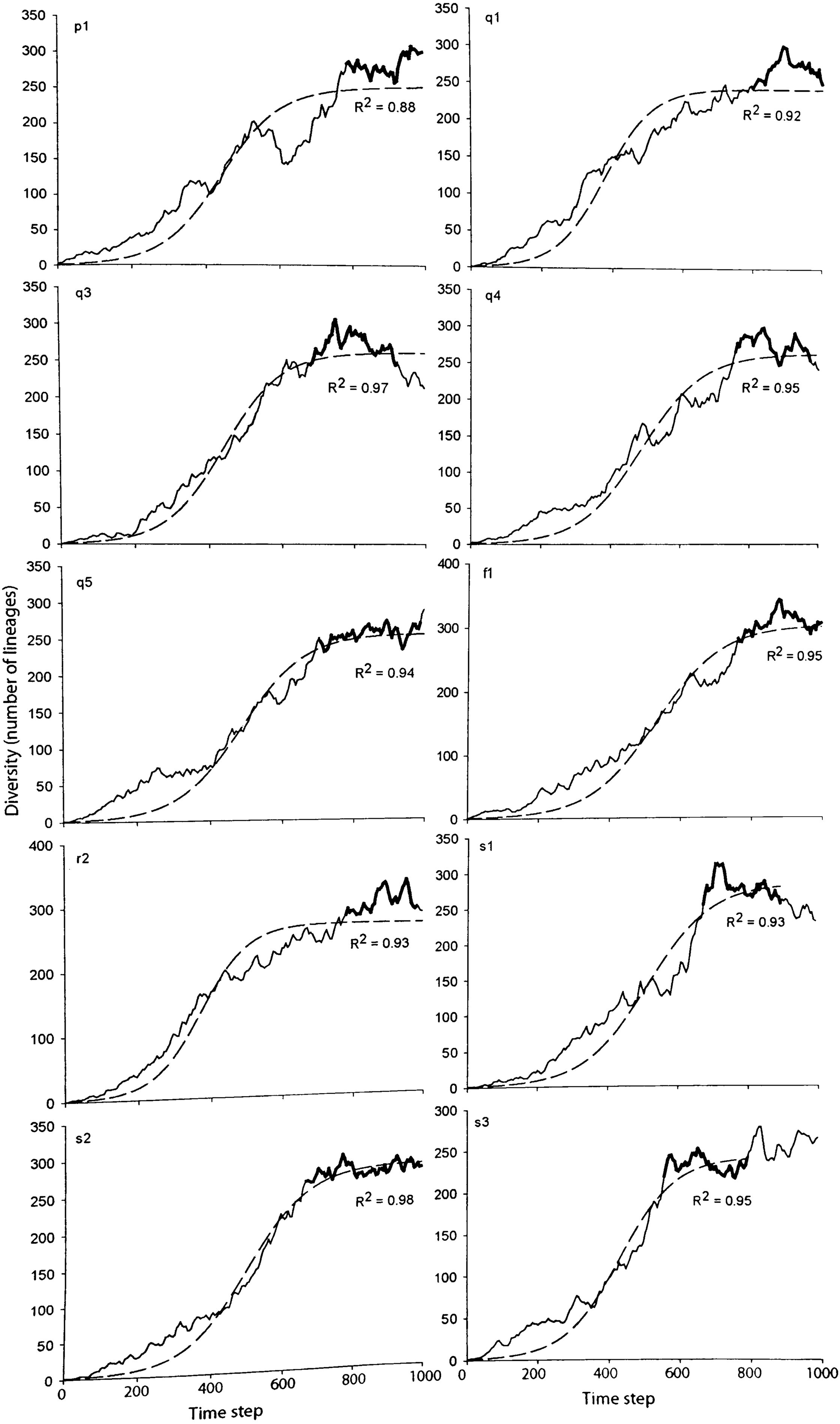
APPENDIX III: CLOCKBACK GRAPHS

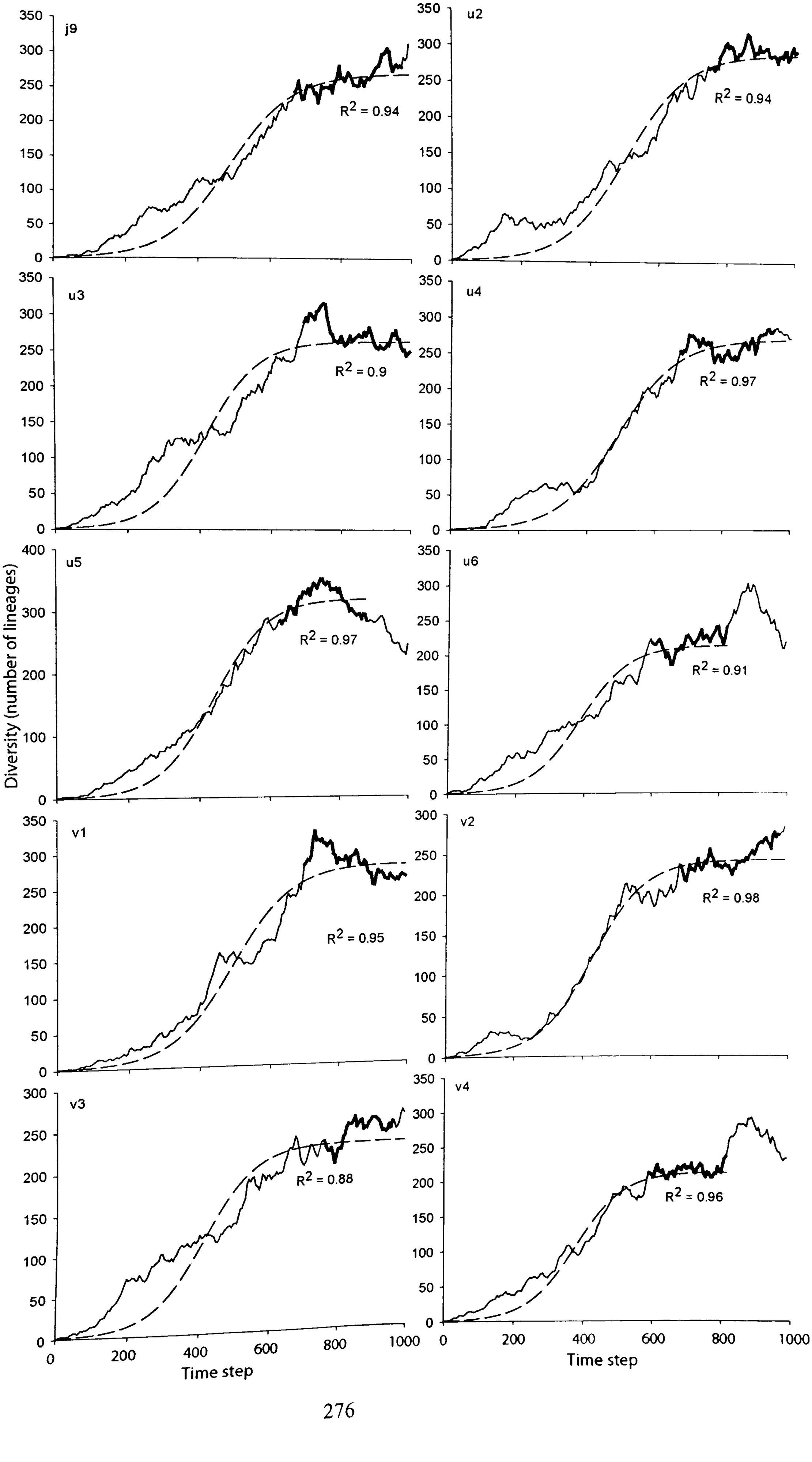
This appendix contains the diversity curves for all sixty-nine of the successful CLOCKBACK trees that include diversity periods fitting 'plateau criteria' (see Chapter 4, Section 4.2.4). The fit of the logistic model and corresponding correlation coefficients are shown in each case. The letters and numbers in the corner of each curve indicate the file name of the CLOCKBACK tree.

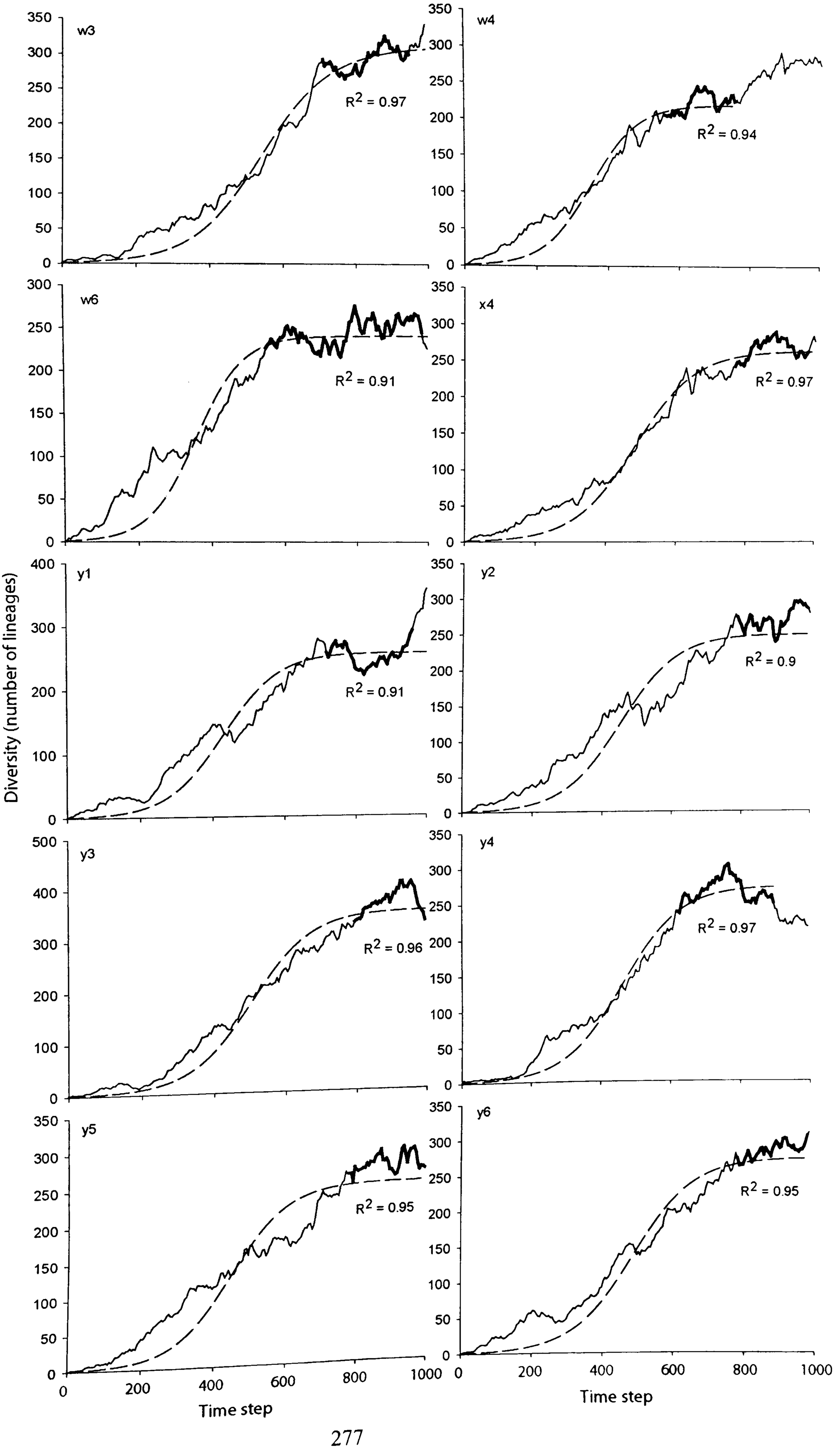


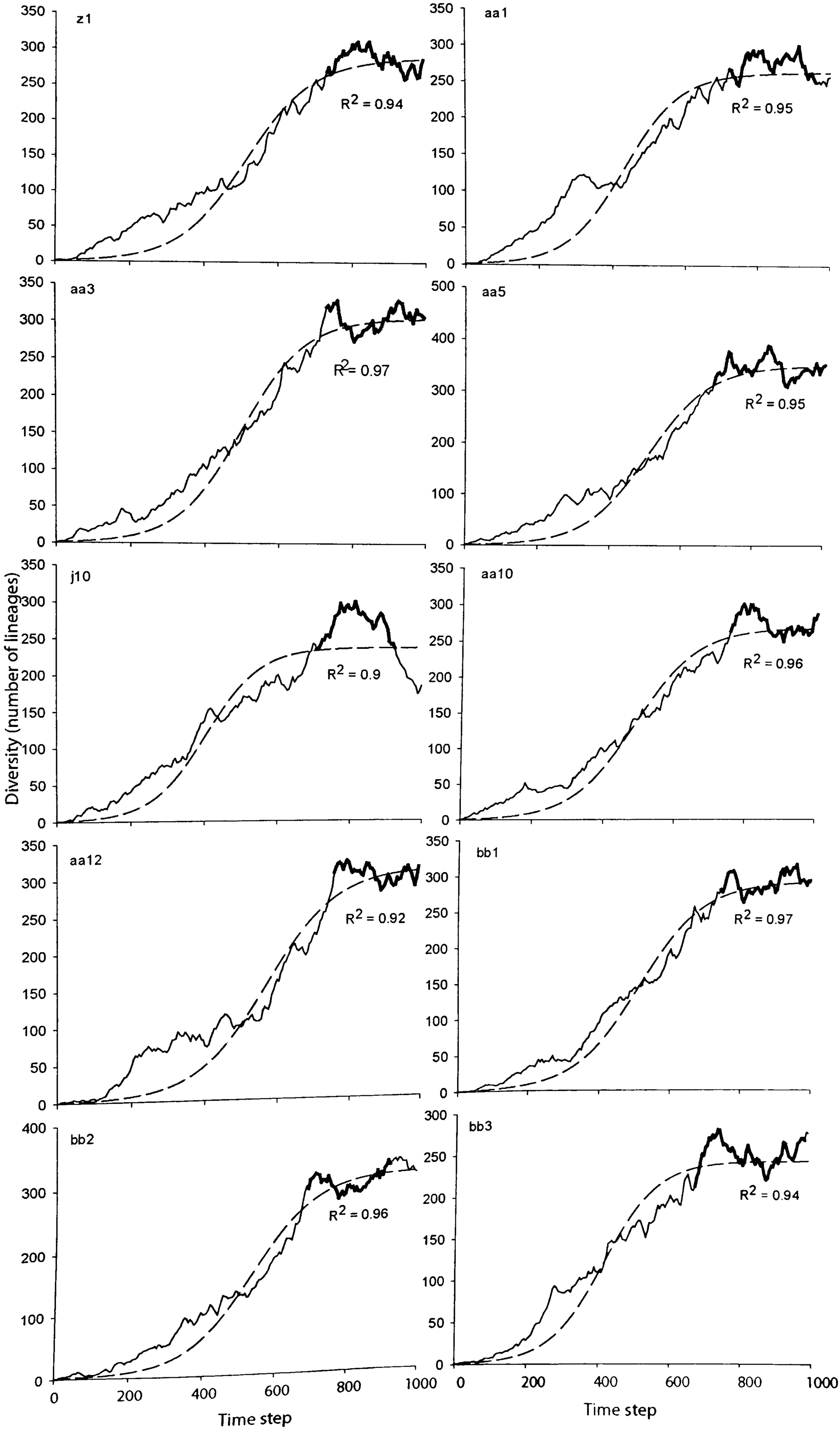

i2
$R^2 = 0.98$
j1
$R^2 = 0.94$
j2
$R^2 = 0.97$
j4
$R^2 = 0.81$
j5
$R^2 = 0.97$
j7
$R^2 = 0.94$
t1
$R^2 = 0.99$
aa9
$R^2 = 0.95$
h3
$R^2 = 0.94$
aa4
$R^2 = 0.96$
Diversity (number of lineages)
Time step

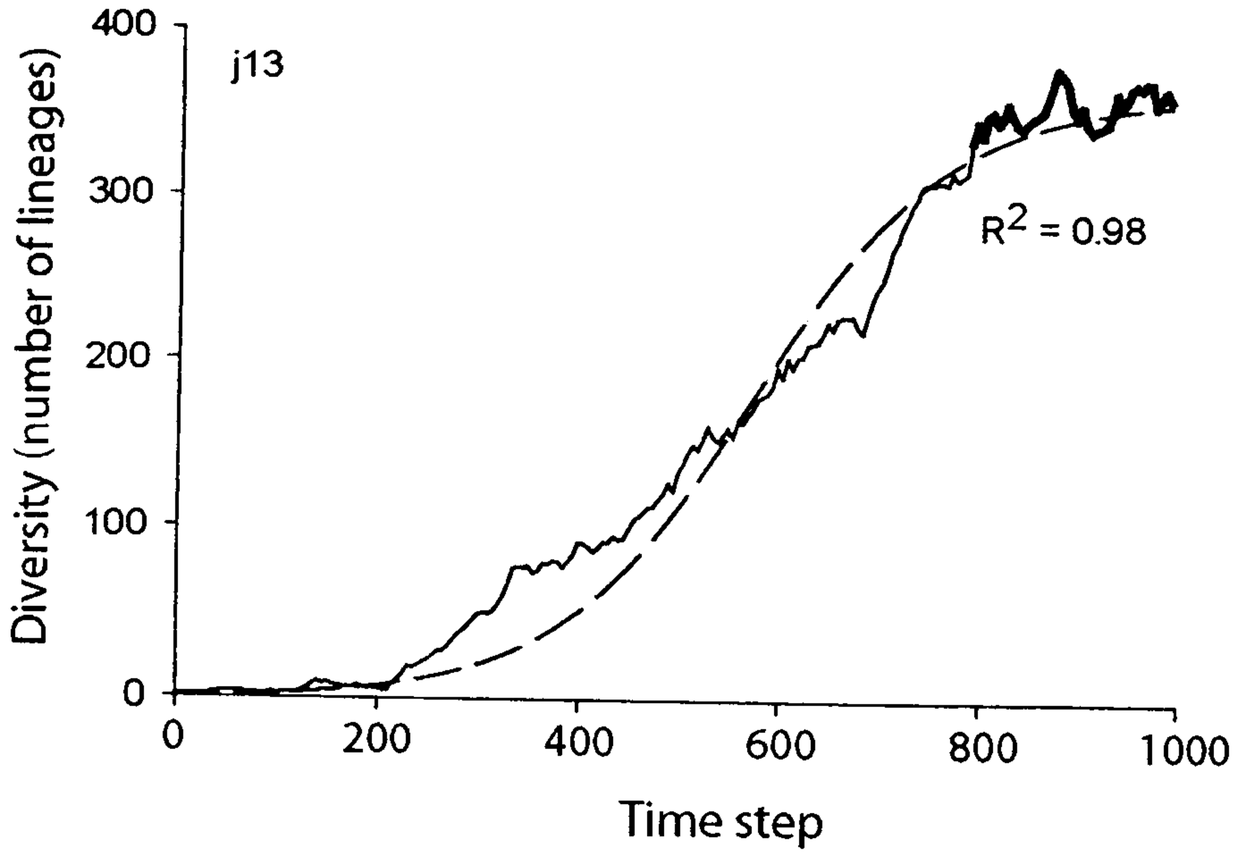

g4
R^2 = 0.94
k2
R^2 = 0.9
h2
R^2 = 0.97
m1
R^2 = 0.95
m2
R^2 = 0.97
m5
R^2 = 0.95
m6
R^2 = 0.91
m7
R^2 = 0.9
o1
R^2 = 0.9
o2
R^2 = 0.96
Diversity (number of lineages)
Time step
Time step


p1
R^2 = 0.88
q1
R^2 = 0.92
q3
R^2 = 0.97
q4
R^2 = 0.95
q5
R^2 = 0.94
f1
R^2 = 0.95
r2
R^2 = 0.93
s1
R^2 = 0.93
s2
R^2 = 0.98
s3
R^2 = 0.95
Diversity (number of lineages)
Time step
Time step


j9
R^2 = 0.94
u2
R^2 = 0.94
u3
R^2 = 0.9
u4
R^2 = 0.97
u5
R^2 = 0.97
u6
R^2 = 0.91
v1
R^2 = 0.95
v2
R^2 = 0.98
v3
R^2 = 0.88
v4
R^2 = 0.96
Diversity (number of lineages)
Time step


w3
R^2 = 0.97
w4
R^2 = 0.94
w6
R^2 = 0.91
x4
R^2 = 0.97
y1
R^2 = 0.91
y2
R^2 = 0.9
y3
R^2 = 0.96
y4
R^2 = 0.97
y5
R^2 = 0.95
y6
R^2 = 0.95
Diversity (number of lineages)
Time step
Time step


z1
R^2 = 0.94
aa1
R^2 = 0.95
aa3
R^2= 0.97
aa5
R^2 = 0.95
j10
R^2 = 0.9
aa10
R^2 = 0.96
aa12
R^2 = 0.92
bb1
R^2 = 0.97
bb2
R^2 = 0.96
bb3
R^2 = 0.94
Diversity (number of lineages)
Time step
Time step


j13
Diversity (number of lineages)
400
300
200
100
0
0
200
400
600
800
1000
Time step
R^2 = 0.98